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Long-term persistence of isolated fish populations in the Alexander Archipelago

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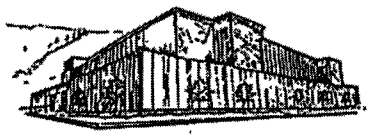

LONG-TERM PERSISTENCE OF ISOLATED FISH POPULATIONS IN THE ALEXANDER ARCHIPELAGO

by

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Long-Term Persistence of Isolated Fish Populations in the Alexander Archipelago

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The "small population paradigm" holds that small population size enhances risk of extirpation, with risk factors grouped as genetic, demographic, and "environmental". To understand the factors that determine likelihood of persistence, I studied coastal cutthroat trout (*Oncorhynchus clarki clarki*) and Dolly Varden (*Salvelinus malma*) populations in southeastern Alaska that have been isolated from immigrants for thousands of generations. These populations became isolated when isostatic rebound following deglaciation created waterfalls.

I developed a geological model of variations in Holocene uplift across the region, and tested it independently using the presence/absence of fish in isolated, high elevation lakes. The model predicted locations where isolated populations should be found above waterfalls. I inferred population persistence over the intervening millennia using presence/absence of present-day populations at these locations.

I examined loss of genetic microsatellite variation in 12 isolated coastal cutthroat trout populations. All populations showed reduced heterozygosity and allelic diversity compared to populations downstream of isolating waterfalls. The genetic variation retained was highly correlated with amount of available habitat. I calculated the effective population size (N_e) from observed loss of heterozygosity and compared this "genetic" population estimate with "demographic" population size estimates (N) calculated from the amount of available habitat. The strong negative relationship between N_e/N ratio and habitat amount I found suggests the smallest populations lost less genetic variation than expected, perhaps due to heterosis.

To examine conditions under which small, isolated populations persisted or failed, I sampled 124 sites with limited amounts of habitat above waterfalls. I found a 90% likelihood that populations of coastal cutthroat trout or Dolly Varden would be present when more than 4.4 km of stream habitat were available, and a less than 50% likelihood of finding either species in less than 1 km of habitat. Dolly Varden consistently achieved much higher densities than coastal cutthroat trout when the other species was absent. This suggests Dolly Varden population sizes were suppressed in the presence of cutthroat trout, presumably by competition. This study demonstrates that the amount of habitat available to a population is a key determinant of population persistence, for reasons both demographic and genetic.

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CHAPTER 1 – Introduction

BACKGROUND

As the footprint of human disturbance on the planet continues to expand, high-quality habitat for all species is steadily being reduced and fragmented, and the likelihood of local populations becoming isolated is correspondingly increased. In light of this, it might seem surprising that few empirical studies have attacked the question of what determines the persistence of isolated populations. On closer inspection, however, it is difficult to identify a truly isolated population of terrestrial vertebrates to study. Birds and aerial insects fly between habitat patches. Even earthbound species thought to be trapped on remnant habitat fragments (Mills 1995) turn out to cross apparently hostile terrain with sufficient regularity that they cannot be called truly isolated (Tallmon et al. 2002). This vagility makes it difficult to separate the influence of migration on a population from the other factors that may constrain its persistence.

Stream fish are among the species most impacted by anthropogenic habitat fragmentation. In recent decades, many populations have become isolated by activities such as dam building, road culvert construction, and dewatering for irrigation. For stream fish, the conservation imperative for understanding how they are affected by long-term isolation is great, yet the question would seem to be difficult to study. Even a small amount of connectivity appears to permit movement by stream fish (Adams et al. 2000), and they are notorious for their ability to quickly colonize or recolonize newly available habitat (Larimore et al. 1959; Meffe & Sheldon 1990; Milner et al. 2000).

This study seeks to fill this void by examining the long-term persistence of populations of stream-resident coastal cutthroat trout (*Oncorhynchus clarki clarki*) and

Dolly Varden (*Salvelinus malma*) in the Alexander Archipelago of southeastern Alaska. These populations are distinguished by being truly isolated from all immigrants, by the great length of time for which they have been isolated, by their relatively pristine setting, and by the large number of similarly situated isolated populations. These characteristics largely result from the mechanism of their isolation.

Most, if not all, isolated fish populations in the Alexander Archipelago are thought to have become established immediately following the retreat of the Cordilleran ice sheet at the end of the Pleistocene epoch. At this time, sea level was higher in most of the region than it has been since, and barriers that currently block fish passage may have been flooded at that time by the ocean. With the falling of sea level and the melting of ice dams, fish populations above barriers became isolated from incoming migrants and remain that way today. Because these resident fish are small, they have largely escaped human notice and their persistence should be explainable without resorting to anthropogenic disturbance factors, except at the largest scale (*e.g.* global climate change).

Although extinction (or extirpation) is fundamentally a stochastic process, Brown (1995) argued that it is possible to identify factors that favor the probability of extinction. Principal among these is small population size, which increases vulnerability to genetic processes such as drift and stochastic environmental events such as catastrophic disturbance. Though they are not predictable, stochastic events are not uncommon. Populations that are not threatened in other ways normally recover from all but the most catastrophic of stochastic events. However, populations that are small, either due to prior stochastic events or deterministic processes, are at increased risk of extinction from the

next stochastic event. Rieman et al. (1993) provided an overview of extinction processes as they relate to resident salmonids. Extinction processes are characterized as deterministic, stochastic, or genetic. Deterministic extinction processes lower survival or growth rates in predictable ways. For instance, destruction of spawning habitat means that fewer fish will be able to find a place to spawn (assuming full utilization of the resource). Extinction, then, can occur through deterministically driving a population out of existence, or by reducing it to the point that it does not recover from a stochastic event. Because stochastic events cannot by definition be predicted, extinction probability is predicted based on deterministic variables and processes that reduce population size.

RESEARCH OBJECTIVES

The purpose of this research was to explore the factors that limit population persistence by examining the fate of small populations of stream-dwelling fish that have been isolated for thousands of generations. I identified a potential set of study populations thought to have been isolated by uplift in southeastern Alaska. My preliminary goals were:

1. To develop a map of Holocene uplift for southeastern Alaska;
2. To develop a physical model for predicting the location of fish populations isolated by uplift; and
3. To evaluate that model with an independent set of biological data.

Once I had developed an objective model for predicting where isolated populations should be found, I interpreted the presence or absence of fish populations in each location as a indication of whether a population in that setting had persisted since

becoming isolated early in the Holocene. My remaining research objectives were to determine:

1. Whether there was genetic evidence that persisting populations were indeed reproductively isolated;
2. Whether the amount of genetic variation lost was correlated with population size and with length of isolation period;
3. Whether the quantitative loss in genetic variation was similar to what we would expect for isolated populations;
4. What were the most restricted settings in which isolated populations are known to have persisted;
5. How well was population persistence predicted by the amount of habitat available and length of isolation period; and
6. Whether the presence or absence of another salmonid species affected the likelihood of population persistence.

In Chapter Two, I develop and evaluate a model for predicting the locations in southeastern Alaska where post-Pleistocene fish populations would have been founded and subsequently isolated. Chapter Three addresses research objectives 1-3 above through genetic analysis of 12 isolated populations of coastal cutthroat trout in contrast with their putative founding population. Chapter Four addresses research objectives 4-6 by contrasting stream and watershed characteristics of settings where isolated populations of coastal cutthroat trout and Dolly Varden are, and are not, found today. The final chapter, Chapter Five, is largely unrelated to the other chapters and derives from an internship I completed as part of my graduate program requirements.

SIGNIFICANCE OF RESULTS

Mechanism of Isolation: Chapter Two and the associated appendix compile all known information about southeastern Alaskan Holocene uplift in one place for the first time, and present new hypotheses about the amount and variation of uplift in the region. Uplift as a mechanism of isolation is added to the list of those more commonly considered, including flooding, fire, desertification, glacial advance, vulcanism, and, especially, anthropogenic landscape disturbance. Uplift is distinguished from most of the others by the relatively slow speed at which it proceeds, the relatively large area affected, and the long time during which its effects persist.

Genetic Variation: This study reports on genetic variation in populations that have been completely isolated by natural means for a far longer period than most studies of the genetic effects of isolation or fragmentation. My results do not contradict the results of other studies, but instead provide strong support for prior conclusions drawn where isolation from immigrants was not as complete or the period of isolation as long. The very high correlation I found between genetic variation and habitat size in isolated populations underscores the importance of reserve size in the preservation of small populations. I report a negative correlation between the ratio of effective population size to census population size, and census population size itself. This pattern could have significant implications for the genetic behavior of populations during bottlenecks.

Habitat Size and Persistence: In Chapter Four, I showed that habitat size was correlated not only with the degree of reduction in genetic variation but with the likelihood of persistence itself. This relationship was so strong that no other habitat

factors I considered were significant in a multiple logistic regression model for prediction of population persistence. The literature of conservation biology is rife with predictions of the correlation of patch size with the so-called extinction threshold (see review in Fahrig 2003), but this study is one of the few to test it empirically, and it underscores recommendations that habitat preservation should be the first priority for conservation (Fahrig 2001). However, I was able to document multiple populations persisting in complete isolation in patches somewhat smaller than others have suggested are required (Harig & Fausch 2002; Hilderbrand & Kershner 2000). There is a tendency among conservationists to write off the future of very small populations unless they are the only remaining population of a species, but my results show that smaller populations may have brighter prospects than have been previously assumed. In Chapter Four, I also demonstrated that the presence or absence of another, similar species can have a marked effect on persistence, and that this degree to which this effect is manifested is not constant among species. Finally, the data I report in Chapter Four provide strong empirical support for the oft-used recommendation that effective population size should be not less than 500 to ensure long-term population persistence.

CONCLUSIONS

Small isolated fish populations offer an unparalleled opportunity to study population persistence in both natural and human-influenced settings. This study adds to the growing body of literature that documents the genetic and demographic impacts of isolation on population persistence. My research is distinguished by the degree to which the populations that I studied are isolated, by the protracted length of the isolation period,

and by the entirely natural mechanism of isolation operating on a scale that resulted in numerous comparable populations distributed across a broad area. Many of my results confirm the concerns that others have raised about the effects of smallness and isolation on the persistence of vertebrate populations, but I have also demonstrated that long-term persistence is sometimes possible in conjunction with greatly reduced genetic variation and highly restricted spatial extent. The populations I studied are not thought to be at short-term risk, making it realistic to undertake longer term studies of their demography that will help to uncover the mechanism for the dependence on habitat quantity that is reported here.

At the same time, these populations have been proposed as indicators of watershed disturbance in southeastern Alaska, rather than the anadromous populations that inhabit the same landscape. Anadromous fish spend a significant part of their lifetimes in the ocean, and ocean conditions are thought to greatly influence population fluctuations (Beamish & Bouillon 1993), possibly to the extent of swamping the effects on population abundance of variation in freshwater habitat. Although Holtby and Scrivener (1989) were able to isolate the effects of ocean conditions on population trends in coho and chum salmon at Carnation Creek, British Columbia, the process required detailed measurements of many demographic parameters that would be impractical to gather on larger spatial scales. The difficulty of obtaining and interpreting such data is the argument for using resident species or populations in preference to migratory ones as indicators of local habitat conditions. By focusing on these previously little-studied populations, my research provides some context for the interpretation of population trends and monitoring data.

Further, one must consider that southeastern Alaskan resident fish populations which once might have been called marginal may now be among the healthiest in the species range, and may perhaps become source populations for recolonization elsewhere. Exotic species introductions have been very limited in southeastern Alaska, in sharp contrast to much of the rest of the world, and thus these populations are less likely to have been impacted by hybridization or selection due to interactions with invaders. This could make them valuable reservoirs of genetic diversity for reintroduction programs, and argues for deepening our understanding of the health, stability, and uniqueness of these populations. Finally, through investigating the genetic structure of isolated fish populations across the region, this study will be of value to natural resource managers considering whether these populations should be considered to be ecologically significant units (ESU's, *sensu* Waples 1991) and accorded corresponding protection.

TWEB INTERNSHIP

The final chapter of my dissertation derives from an internship I did with the Tongass National Forest (U.S.D.A. Forest Service). At the University of Montana, I was supported by an NSF Graduate Research Traineeship in the Training within Environmental Biology (TWEB) program. This program required that students complete an internship outside academia that did not duplicate their other research and that provided opportunities for linking basic science with application. For my internship, I participated in an interagency working group charged with establishing a monitoring and evaluation program for the comprehensive management plan that governs all activities on the Tongass National Forest (USDA Forest Service 1997). This plan, which was

finalized at about the time I began my graduate program, was the first to include research scientists as full members of the U.S. Forest Service planning team (Mills et al. 1998). A centerpiece of the plan was a progressive conservation strategy based on a network of reserves along with habitat protection measures governing development outside the reserves. The scale of the plan – the Tongass National Forest covers 17 million acres, including most of the southeastern Alaska panhandle, and is by far the largest National Forest in the United States – and the emphasis on habitat conservation and ecological sustainability distinguished this plan from all previous National Forest management plans (Everest *in press*). Monitoring and evaluating the success of a natural resource management policy at that scale was, and is, a formidable challenge, particularly because the policy is implemented incrementally across space and time, and continues to evolve while it is being evaluated. The monitoring questions asked of researchers tend to be intractably large and complex by the standards of institutional science, and the timeframe for answering them is short. An operational framework is needed to guide collaborating natural resource managers and scientists towards monitoring activities that are both meaningful and tractable. In my internship report, I offer such a framework, using the Tongass National Forest conservation strategy as a case study of how the effectiveness of large, distributed reserve networks might be most productively and efficiently evaluated.

CHAPTER 2 – Natural Mechanisms of Population Isolation:

Salmonids and Uplift in Southeastern Alaska

ABSTRACT

Human activities often fragment habitat for other vertebrate species, and as a result can create isolated populations at risk of extirpation or even extinction. However, natural processes can also isolate populations, without any human intervention. Flooding, fire, desertification, glacial advance, and vulcanism are among the natural processes that can sever ties among previously interconnected habitats. For stream-dwelling fish in southeastern Alaska, isostatic rebound has played this role, exposing waterfalls along stream channels previously submerged beneath the sea, and leaving the fish above isolated from upstream immigration. Radiocarbon dates for uplifted marine sediments indicate that most post-Pleistocene uplift in the region occurred more than 8,000 years ago. To predict where present-day isolated fish populations might be found, we used over 100 elevations of exposed marine sediments to map uplift across the region, then identified fish habitat above waterfalls below the maximum uplifted elevations. We evaluated these predicted locations for isolated fish populations by comparing them with presence/absence data for 350 lakes blocked from upstream immigration. Uplifted marine sediments are found up to 230 m (750') above present day sea level, while the highest isolated natural populations of lake fish are at 245 m (800'), closely matching the predictions of our geological uplift model. We identified three uplift zones, ranging from the mainland where the ice was thickest and isostatic rebound greatest, to the outer coast where rebound was generally less than 60 m (195'). Lake fish populations were often

found somewhat above the highest known uplifted sediments in a region, not surprisingly since our lake fish inventory is larger and more systematically distributed than the incidental observations of uplifted marine sediments. We modified our uplift model to include the south end of Prince of Wales Island in the medium-uplift zone based on medium-elevation isolated fish populations found there. This placement is consistent with recent evidence that a large tongue of ice extended out of Dixon Entrance, immediately to the south of Prince of Wales Island. Our uplift model predicts that southeastern Alaska could contain hundreds of naturally isolated fish populations, making the region an ideal laboratory to study the conditions under which small, isolated salmonid populations are able to persist, with implications for population viability of other species in other settings.

INTRODUCTION

As increasing exploitation of resources by humans leads to landscape transformation, the availability of interconnected habitat for many species is increasingly reduced, and the likelihood of local populations becoming isolated is correspondingly increased. In the struggle to preserve global biodiversity, an understanding of the factors that influence the persistence of small, isolated populations is a critical need. In light of this, it might seem surprising that relatively few studies have attacked this question for natural populations. On closer inspection, however, it is difficult to locate a truly isolated natural population of terrestrial animals to study. Birds and aerial insects fly between habitat patches. Even earthbound species thought to be trapped on remnant habitat fragments cross apparently hostile terrain with sufficient regularity that they cannot be

called truly isolated. This vagility makes it difficult to separate the influence of migration on a population from the other factors that may constrain its persistence.

Stream fish are among the species most impacted by anthropogenic habitat fragmentation (Martin-Smith & Laird 1998; Warren & Pardew 1998). In recent decades, many populations have become isolated by activities such as dam building, road culvert construction, and dewatering for irrigation. For stream fish, the conservation imperative for understanding how they are affected by long-term isolation is great, yet the question would seem to be difficult to study. Even a small amount of connectivity appears to permit movement by stream fish (Adams et al. 2000), and they are notorious for their readiness to quickly colonize or recolonize newly available habitat (Bayley & Osborne 1993; Larimore et al. 1959; Meffe & Sheldon 1990; Milner et al. 2000). For these and other reasons, the literature makes almost no mention of attempts to address the persistence question for stream fish in the absence of a metapopulation structure. In southeastern Alaska, however, there appear to be large numbers of similarly sized, small populations of native fish that are completely isolated from immigration. These populations offer an unusual opportunity for study. Isolated fish populations occur in other settings (Pister 1985; Waters & Wallis 2001) but naturally isolated stream fish populations in southeastern Alaska are distinguished by at least three important characteristics: (1) the setting they are found in is relatively pristine, so that natural processes can be examined without the complications of anthropogenic influence; (2) southeastern Alaska contains numerous isolated fish populations, allowing for study replication and stronger inference; and (3) there is no immediate threat to the persistence of many populations, making long term studies a viable option.

Quaternary History of Southeastern Alaska

Nearly all of the Alexander Archipelago and associated mainland coast of southeastern Alaska was covered by the Cordilleran ice sheet during the late Pleistocene epoch, in contrast with conditions in the large Beringian refugium to the north and in small glacial refugia immediately to the south on Haida Gwaii (Queen Charlotte Islands) (Demboski et al. 1999; Heusser 1989; Moodie & Reimchen 1976). In southeastern Alaska it is likely that only the highest mountains on the larger islands and a few portions of the outer coast were ice-free during the glacial maximum (Heaton et al. 1996; Mann 1986). Upper limits of ice action range from 600 m along the outer coast to 1500 m at the edge of the mainland (Falconer et al. 1958, cited in Heusser 1989). Limited evidence for the existence of Pleistocene glacial refugia in this region includes animal remains found in caves on western Prince of Wales Island (black and brown bears, *Ursus* spp., Heaton et al. 1996), and disjunct present-day plant distributions (subalpine fir, *Abies lasiocarpa*, Heusser 1989). However, Worley and Jaques (1975) argued that the distribution of subalpine fir is more suggestive of post-Pleistocene recolonization from the south or the continental interior than of local coastal refugia.. Locations of possible glacial refugia include steep-sided Forrester Island (Worley & Jaques 1975), on the outer coast 26 km west of its nearest neighbor, and presently submerged portions of the continental shelf that were exposed by lowered sea levels. The latter may have been occupied or used as travel corridors by humans (Klein 1965; Rogers et al. 1990). However, to date there have been no suggestions of freshwater fish refugia in southeastern Alaska, and no relict fish populations have been identified south of Yakutat

(the exception being a possible relict population of northern pike, *Esox lucius*, near Yakutat, Senanan & Kapuscinski 2000). While the presence of relicts cannot be ruled out, it is reasonable to expect that most freshwater fish populations in the region have been established since the retreat of the Cordilleran ice sheet.

Absent refugia, the only source from which the streams lying wholly within southeastern Alaska could have been colonized is the sea. (A few rivers, such as the Stikine and Taku, penetrate the Coast Range and could have been colonized from continental refugia, but their only connection to the remainder of Archipelago streams is through saltwater.) Access to individual streams would have been determined by local sea level. Relative sea levels in the region fluctuated dramatically following the retreat of the Cordilleran ice sheet, determined both by worldwide eustatic variation and by local isostatic rebound. Worldwide eustatic lowering of sea level during the last glacial maximum, around 18,000 BP, was on the order of 120 m below present sea level (Fairbanks 1989), exposing many continental shelves. The maximum extent of the Cordilleran ice sheet was reached somewhat later. Barrie and Conway (1999) dated the beginning of the retreat of the ice sheet to about 15,600 14C yr BP. (By convention, radiocarbon dates without an associated error are uncalibrated and relative to 1950 A.D. See Stuiver & Polach 1977.) Most glaciers in the Alexander Archipelago are thought to have retreated rapidly to near their present positions by about 13,500 14C yr BP (Barrie & Conway 1999; Mann & Hamilton 1995). Specific dates for the retreat of the ice from various parts of the Archipelago range from 12,900-10,500 14C yr B.P. (Mann 1986). Local dates of retreat given by Mann (1986) suggest an obvious west-to-east progression for the retreat, but no similar pattern from south to north.

Colonization by Salmonids

As a group, salmonids embody many of the traits that characterize successful colonizers, including reproduction at an early age, high fecundity, generalist spawning strategies, high vagility, and high tolerance for the kind of conditions found in recently disturbed settings, such as turbid water. Milner and Bailey (1989) examined five streams in Glacier Bay, Alaska that were exposed by retreating glacial ice from zero to 150 years earlier, all of which had already been colonized by one or more species of salmonids. Dolly Varden char (*Salvelinus malma*) were the most ubiquitous colonists, being found in all streams where other fish species were detected and on all occasions when other fish were present. In contrast, cutthroat trout (*Oncorhynchus clarki*) were recorded only in small numbers in the stream that was oldest and farthest along in the successional process. Other salmonids were intermediate between the two species in their colonization pattern. Recent unpublished observations in additional streams confirm this pattern (A. Milner, *pers. comm.*) It is likely that salmonids would have rapidly colonized all available habitat in southeastern Alaska not long after the retreat of ice in the region. It is rare to find a stream in the region today that has saltwater access but does not contain Dolly Varden char, cutthroat trout, and one or more species of salmon.

Isolation of Fish Populations

Figure 2.1 illustrates the process of isolation. Following colonization, isostatically depressed shorelines rebounded dramatically. Within southeastern Alaska, marine transgressions of 50-230 m above present sea level indicate the magnitude of the

apparent rebound (Mann 1986; Mann & Hamilton 1995). Actual rebound was even greater, however, since the elevation of marine transgressions is reduced by the concomitant eustatic rise in worldwide sea level. Between 13,000 and 9,000 14C yr B.P., evidence suggests a eustatic rise in sea level from –105 to –35 m below present (Fairbanks 1989). For much of the region, isostatic rebound ran its course within a few thousand years. Mann and Hamilton (1995) speculated that, in general, modern sea level in southeastern Alaska was reached by 9,000 14C yr B.P., except where isostatic or tectonic forces continued to be active. Riddihough (1982) believed that isostatic movements on the west coast of Canada were largely complete by the early Holocene (11,000 to 8,000 B.P.). However, eustatic rise of sea level continued into the middle Holocene, so some shorelines should not be considered completely stable until about 5,000 B.P. In the time since, they have varied by only a few meters (Clague 1989; Riddihough 1982).

Few data on sea level changes are available for southeastern Alaska, but a pattern of high variability is evident. A marine transgression occurred on Heceta Island around 8,500 B.P., but no evidence of this event has been found on the west coast of Prince of Wales Island, which lies immediately to the east of Heceta (Mobley 1988). Mann (1995) and Mann and Hamilton (1986) described early Holocene marine transgressions of 50-230 m above present sea level from a variety of locations within the Archipelago, with a similar west-to-east pattern as is seen in northwestern British Columbia. Hicks and Shofstal (1965) mapped emergence rates for the northern Alexander Archipelago during the first half of the 20th century and found that uplift was greatest at the northern end of the Archipelago, almost 4 cm/yr in Glacier Bay, decreasing to as little as 0.15 cm/yr near

Kake in the center of the Archipelago. For the mid-Holocene, Mobley (1988) summarized 21 carbon-dated marine deposits ranging from 1-70 m above sea level.

In general, absent detailed local geological history or evidence of recent barrier formation, we can expect the isolation of fish populations on most islands in southeastern Alaska to date to about 9,000 B.P. (Clague et al. 1982; Mobley 1988) and even in unusual cases to at least 5,000 B.P. (Clague 1989; Riddihough 1982). Also, we would expect to find no populations in waters that are not continuously connected to the maximum historical elevation of marine transgressions.

Objectives

Our overall objective was to identify a set of naturally isolated, small populations that would allow us to study the factors affecting long-term population persistence, using salmonids historically isolated above waterfalls in southeastern Alaskan. Because we were interested in very small populations, we focused our attention on headwater drainages that did not include ponds or lakes (since those should support much larger fish populations). However, we also collated data about fish presence in lakes to test our predictions. Our specific objectives were: (1) to develop a map of Holocene uplift for southeastern Alaska; (2) to predict locations where one would expect to find isolated fish populations, based on the uplift map and GIS hydrography for the region; and (3) to test these predictions using the presence or absence of natural fish populations in isolated *lakes*. We then used our uplift model to characterize the set of predicted locations where isolated *stream* fish populations would be expected.

METHODS

Study Area

Southeastern Alaska is a distinct ecoregion that comprises the Alexander Archipelago and the associated mainland coastline. It is bounded on the west by the open Pacific Ocean and on the east by a nearly unbroken range of mountains. To the north, the Archipelago comes to an end and is replaced by sweeping sandy beaches. On the south, the Archipelago stops at Dixon Entrance, a broad body of water that approximately defines an ecotone representing the northern limit of a number of terrestrial species. McPhail & Lindsey (1986) identified the Stikine River, which flows westward to the ocean about halfway up the Tongass, as transitional between the Columbian ichthyofauna to the south and the Bering icthyofauna to the north.

The mainland coast here averages about 50 km in width, as measured from saltwater inland to the peaks of the Coast Range, which form the boundary between Alaska and Canada. The region covers approximately 500 km of latitude and 150 km of longitude, and it includes over 22,000 islands by one estimate (USDA Forest Service 1997). It is steep, rugged terrain partitioned by deep fjords, with a temperate rainforest climate dominated by the frequent arrival of storms off the North Pacific. Rainfall ranges from 130 - 600 cm/yr (Alaback 1995), feeding a network of about 72,000 km of mapped streams, of which approximately half are considered fish-bearing (USDA Forest Service 1997). Streams within the Archipelago tend to be very similar to one another: wooded, short, steep, bedrock-controlled in their upper reaches, and subject to similar hydrologic regimes. Virtually every stream is inhabited by fish, chiefly salmonids, in its lower reaches. With a very few exceptions, most fish species present in the Archipelago are

found throughout the region (Morrow 1980). For the purposes of this study, it is noteworthy that there is an extensive geographical database available for the entire region that is particularly rich in hydrological information and landform characteristics relevant to the study questions.

Uplift Model

We used present-day elevations of uplifted glaciomarine sediment deposits to map Holocene uplift across southeastern Alaska. For this study, we did not collect any new records of glaciomarine deposits; rather, we surveyed the published literature and interviewed scientists currently investigating the recent geological history of the region to compile a comprehensive list of all known locations of uplifted glaciomarine deposits (Appendix 1). To determine the range of uplift for each area within the region, we grouped these locations into approximate spatial clusters. Within each spatial cluster of data points, we considered the maximum recorded uplift value as the minimum amount of uplift expected for that area. Because of the paucity of records of uplifted glaciomarine sediments throughout this large region, however, we were only able to distinguish three uplift zones.

To establish the time when sediments were originally deposited, we used radiocarbon dates for shell, or sometimes wood, fragments found within or above the glaciomarine sediments. We report conventional radiocarbon ages (*i.e.* uncalibrated and relative to 1950 A.D.; Stuiver & Polach 1977). The time of deposition of the sediments establishes the maximum amount of time that could have elapsed since a site at that

elevation emerged from the sea. To avoid confusion with earlier uplift events, we considered only marine sediments deposited during the Pleistocene.

Upstream Migration Barriers

To identify upstream migration barriers across the region, we started with an existing GIS barrier layer created by examining aerial photographs of the Tongass National Forest to detect apparent geological discontinuities along stream channels (GIS "barriers" layer, Tongass National Forest,1999). We added hundreds of barriers to the layer by reviewing all available written stream surveys conducted by state and federal agencies between 1950 and 2000; the primary objective of these surveys was generally to determine the upstream limit of anadromous fish presence. Our intent was to consider only barriers that permanently block all upstream migration by all fish species found in this region, as defined by USDA Forest Service (2001a: 22.6, Exhibit 01, p. 14). Although we ground-truthed only a small percentage of the barriers identified by previous surveys, we are confident based on that experience that most of the barriers identified do indeed block fish. We eliminated, for obvious reasons, any barriers where anadromous fish were reported upstream. In addition to individually mapped barriers, we also considered stream segments mapped in three channel types to be *de facto* upstream movement barriers. These channel types were: HC5 and HC6, non-incised and incised channels that have minimum gradients of 15% but generally steepen rapidly beyond that point; and MC3, a 6-15% gradient bedrock-controlled channel type that almost invariably includes frequent stepped cascades (USDA Forest Service 1992). Elevation at the top of

all mapped and de facto barriers was visually estimated to the nearest 25' (7.5 m) from mapped 100' (30 m) contours derived from a 60m digital elevation model (DEM).

Isolated Lake Fish Populations

Presence/absence of natural fish populations in lakes was determined from lake survey files maintained mostly by the Alaska Department of Fish and Game. Lake surveys were conducted during the period 1950-1990, using a variety of methods (minnow trap, gillnet, fyke net, rod & reel, and visual observation). Surveys generally attempted to distinguish natural from stocked populations, although unrecorded stocking undoubtedly occurred in the region and could confound some reports. Dates of stocking events and the results of later surveys to establish their success were sometimes available. We used barrier information in both the lake survey files and the Tongass GIS to establish which lake populations were isolated. Outlier records of populations at extremely high elevations were inspected and removed from the data set wherever recent concentrated human access or recorded stocking activity provided circumstantial evidence for artificial translocations. The elevations of natural fish populations in lakes above barriers were used to test the predictions of our uplift model, *i.e.* that fish would not be expected in lakes with barriers above the local maximum uplift elevation. Also, while it was not an explicit objective of this study, the lake fish presence/absence data also offered the opportunity to establish the maximum elevation at which natural and stocked fish (not merely isolated populations) are present in southeastern Alaska.

Identification of Predicted Sites for Isolated Stream Fish Populations

We considered any fish habitat above a barrier that was not higher than the local maximum predicted post-Pleistocene sea level to hold potential for supporting an isolated fish population. We used the Tongass National Forest's GIS "streams" layer – which was generally derived from aerial stereo photointerpretation, supplemented by extensive ground truthing -- to locate fish habitat above barriers. We used GIS stream channel type attributes (minimum map unit = 100m of linear channel) to identify fish habitat. All mapped stream segments of channel types other than the highest gradient channel types (HC5, HC6 and MC3) were considered capable of supporting fish (USDA Forest Service 1992).

Elevation to the nearest 25' (7.5 m) was visually estimated for the top of all mapped and de facto barriers, using mapped 100' (30 m) contours derived from a 60m digital elevation model (DEM). We measured the amount of fish habitat (to the nearest 50m) above any barriers whose top elevation did not exceed the maximum predicted amount of uplift for the zone they were in, continuing to the upstream limit of fish habitat or to the next barrier whose top elevation was above the maximum uplift elevation.

Because of GIS limitations, we were required to examine the database manually for instances of stream fish habitat above barriers, and thus did not attempt to identify all such instances. We restricted our examination to the northern and central portions of the Archipelago because of the greater accuracy of steam data for these areas.

RESULTS

Uplift Model Based on Geological Evidence

We located 81 previously published records of either post-Pleistocene uplifted glaciomarine sediment deposits or landforms indicative of historical shorelines. An additional 39 unpublished records of sites with evidence of uplift were contributed by archaeologists and geologists of the Tongass National Forest (Appendix 1). The highest known glaciomarine deposit in southeastern Alaska is at 230 m (750') ASL on the mainland near Juneau. Broadly speaking, documented uplift is greatest at the northern end of the archipelago, and greater near the mainland than the outer coast. This pattern is consistent with the expectation of greater ice sheet thickness over the mainland than the islands. Undoubtedly there was significant local variation in ice sheet thickness throughout the region and consequently in subsequent isostatic rebound (D. Swanston, *pers. comm.*), but the sparseness of the glaciomarine sediment deposit record in southeastern Alaska does not allow for interpretation at this scale. Instead, we chose to delineate three uplift zones for the region (Figure 2.2).

We placed all of the outer coast islands in the first uplift zone. No uplifted marine sediments were found at greater than 20 m (66') ASL in this zone, so we believed that uplift here was likely to be generally less than 30 m (bearing in mind that 20 m would be a *lower* limit on the amount of uplift for this zone). In the second zone, we placed the mainland west of Lynn Canal and the remainder of the islands. Twelve of 25 documented uplift sites in this zone exceeded 30 m ASL, and five of those exceeded 60 m ASL. The maximum uplift noted was a rough estimate of 90 m ASL for one site on Revillagigedo Island near the mainland, so we believe that uplift in the intermediate zone

was generally less than 100 m. The remaining, high-uplift zone consists of the mainland east of Glacier Bay, along with the Lynn Canal area, Douglas Island near Juneau and the Mansfield Peninsula at the north end of Admiralty Island. The latter two areas are included in this zone because they are geologically associated with the Lynn Canal mainland. As well, both contain uplift sites well above 100 m ASL, and the Mansfield Peninsula in particular includes a well authenticated uplift site at 213 m (695') ASL (Miller 1973b), setting it clearly apart from islands in the intermediate zone.. Nine sites in the high-uplift zone were above 100 m ASL, at elevations ranging from 106 to 230 m ASL. We believe that 230 m is a reasonable estimate for the maximum amount of uplift in this zone.

Isolated Lake Fish Populations

Information about fish presence was available for 531 lakes in southeastern Alaska, of which 269 are known to be isolated from saltwater by upstream movement barriers. Surveys conducted during the period 1951-1994 found apparently natural populations of cutthroat trout and/or Dolly Varden char in 113 of the 269 isolated lakes (42%). The highest lake with a natural, isolated fish population was Boundary Lake (247 m or 804' ASL), in the Taku River drainage on the mainland near the Canadian border. This and other high elevation lakes (over 150 m ASL) were inhabited mainly by Dolly Varden. Scenery Lake, on the mainland near Petersburg, contained Dolly Varden at 295 m (962') ASL, but the migration barrier was further downstream, at 215 m ASL. The highest reported population of cutthroat trout, as well as threespine stickleback (*Gasterosteus aculeatus*), was in Saks Lake (176 m or 574' ASL), also on the mainland

near the mouth of the Unuk River. The only other native fish populations reported from isolated lakes were sculpin (*Cottus* spp.) and kokanee (*Oncorhynchus nerka*, both from lakes at 110 m ASL and below. No native fish were detected in any of the 128 surveyed lakes above 247 m ASL. Because we found no fish populations above this elevation and numerous populations below, we are fairly confident that 245 m ASL represents the approximate upper limit at which native fish populations are sustained in southeastern Alaska. Lakes above that elevation may contain fish, but only if those fish have access to lower elevations through continuously connected stream habitat.

Stocking attempts, from 1921 onward, were reported for 201 lakes, 33 of them above upstream migration barriers. The majority of stocking attempts were in two areas, on Baranof Island south of Sitka and within an 85 km radius circle centered on Ketchikan, with smaller clusters near Juneau and Petersburg-Wrangell. Interestingly, there are at least a few records of stocking for virtually every species known from the region, although some of those events were accidental when a non-target species was unintentionally introduced at the same time as a target species. Non-native species known to have been stocked in southeastern Alaska lakes include eastern brook trout (*Salvelinus fontinalis*) and arctic grayling (*Thymallus arcticus*). Rainbow trout or steelhead (*Oncorhynchus mykiss*) are naturally present in the region in streams and lakes connected to saltwater, and have been widely stocked in isolated lakes as well. A single unstocked isolated lake population of rainbow trout was reported from the eponymously named Rainbow Lake on the Cleveland Peninsula, but it is entirely possible and rather likely that this population was actually the result of an unreported stocking event. The highest elevation where stocking efforts were reported as successful was Lake Dorothy in

the Taku River drainage (952 m ASL), where an isolated population of eastern brook trout stocked in 1921 continues to thrive (Table 2.1). This represents the known, regional upper elevation limit of fish persistence when species and mechanism of colonization are not considered, although the limit could be even higher since no unsuccessful stocking attempts were reported from any higher elevations. As predicted, this elevation (952 m ASL) is substantially higher than that of the highest natural population of any species.

Uplift Model Based on Biological Evidence

The highest natural, isolated, lake fish populations were all below 245 m, which is consistent with the maximum uplift of 230 m documented with geological evidence. Furthermore, the highest populations were generally found on the mainland, which is consistent with the evidence that uplift was greatest near the mainland. In the "Mainland" uplift zone, the highest of 39 reported isolated lake fish populations (247 m ASL) was within the expected elevation range for that zone. The elevation range for the "Inner Islands" uplift zone was likewise generally supported by the 34 reported isolated lake fish populations, with only two populations (one at 107 m ASL on Admiralty Island, and one at 115 m ASL on Kupreanof Island) slightly higher than would be predicted from the geological evidence.

However, along the Outer Coast, isolated fish populations were reported from a number of lakes well above the 30 m ASL we expected, based on the available geological evidence. On Baranof and Chichagof Islands, lakes with fish above 60 m ASL were reported from four drainages. On southern Prince of Wales Island, three lakes were reported with isolated fish populations at 75-125 m ASL. No marine sediment deposits

have yet been found in these areas – the marine sediment dataset and the lake fish dataset are both relatively sparse and uneven across the region – so we cannot say whether the lake fish data conflict with the geological data. Because of this uncertainty, we have constructed a second map of uplift zones that incorporates the additional information provided by the elevations of isolated lake fish populations (Figure 2.3).

Differences between the two uplift maps are summarized in Table 2.2. The differences are both quantitative and qualitative: the biological evidence suggests greater uplift in general; and in a few areas there is evidence that it has been differentially greater than is supported by the distribution of known uplifted glaciomarine sediments. The data points in the set of isolated lake fish populations are both more numerous and more evenly distributed across the region. The fact that isolated lake fish populations occur at higher elevations in general than the record of uplifted glaciomarine sediments would suggest is likely due to undersampling of the latter. In other words, we expect that uplifted sediments would be found at higher elevations if more effort were expended. The explanation for the qualitative differences between the two uplift maps is discussed below; however, it is important to note that both datasets are sparse, given the size and topographic complexity of the region and its history.

Time of Isolation

Of the sites with uplifted marine shell deposits, 57 (47%) are accompanied by a radiocarbon date that records the time that the deposit was laid down in a marine environment (Figure 2.4). Regionwide, the dates range from 7,130+/-115 to 13, 450+/-190 BP (measured radiocarbon date). These dates place a bound on the maximum length

of time elapsed since a site was under saltwater. The fact that there are no dates less than 7,000 BP indicates that post-Pleistocene isostatic rebound had largely tapered off regionwide by that date. Many submerged areas would have emerged from the sea much earlier.

From the larger dataset of radiocarbon-dated, exposed glaciomarine sediments, we selected the most recent date found in each 15 m vertical elevation band and regressed it on log-transformed elevation to produce a formula for predicting the time that a given elevation emerged from the sea during Holocene uplift (Figure 2.5). This regression was highly significant ($p = 0.00004$). Although data points at different elevations were drawn from different parts of the region for this regression, the unambiguous relationship between elevation and sediment deposition date suggests that a single formula for estimating isolation time can be applied regionwide (Hastings 2005, ch. 4).

Isolated Stream Fish Habitat

For the central third of the Archipelago, we identified 593 sites where fish habitat was available above a barrier. This set of sites is incomplete, as we were specifically looking for sites well below the maximum predicted uplift elevation and with very small amounts of habitat above the barrier. We did make a complete examination of four representative islands (Table 2.3), and found approximately one site with isolated fish habitat in the uplift zone for about every 2000 ha of land area. This figure would be somewhat less for the mainland and northwestern portion of the Archipelago because of the steeper topography there; isolated stream habitat in those regions is more often at too high an elevation to expect fish to be present. The linear amount of mapped fish habitat

above these barriers ranges from 100 m (the minimum map unit size for stream channel types) to over 35 km, with sites well-distributed across the entire range.

DISCUSSION

Uplift Models

The general pattern of increasing uplift from the outer coast toward the mainland was supported by both geological and biological evidence. However, we were initially surprised to find reports of fish at such high elevations on the outer coast and especially the southern end of the Archipelago. Recent bathymetric mapping has revealed the existence of submerged glacial troughs at the mouths of the major inland marine waterways of southeastern Alaska, and suggested that Pleistocene glaciation extended as far west as the western edge of the continental shelf (Carrara et al. 2002). Dixon Entrance, which forms the southern boundary of southeastern Alaska, was apparently entirely filled with ice that extended more than 50 km west of present-day shorelines. If that were the case, the ice could easily have been thick enough at the southern end of the Archipelago to explain the existence of uplifted, isolated populations at the elevations reported there. The amount of rebound suggested by the higher lake fish populations implies ice thicknesses of more than 1 km for the inner islands (T. Ager, *pers. comm.*), which is consistent with evidence of ice thickness from glacial trimlines (Mann 1986) and from high elevation deposits on Prince of Wales Island of glacial till (Mann 1986, citing Swanston 1969).

At the north end of the Archipelago, a glacial trough at the outlet of Chatham Strait could explain the presence of high elevation lake populations at the southern end of

Baranof Island, the other area where lake fish were found at higher elevations than predictions based on uplifted marine sediments. Glaciomarine sediment deposits are, however, far more conclusive evidence of uplift than the presence of isolated fish populations that could arguably have other origins. Strandflat topography on the outside of Baranof Island is another indication that uplift could be as much as 75 m on this portion of the outer coast (Reed & Coats 1941), but this too is less conclusive evidence than actual glaciomarine deposits. For the moment, both of the uplift models we present should be thought of as valid hypotheses in need of further testing.

Uplift as a Mechanism of Isolation

Isostatic rebound may function as a mechanism of isolation in other high latitude regions of the Northern Hemisphere. The Cordilleran ice sheet extended through southcentral Alaska to the Alaska Peninsula. Kodiak Island, in particular, has a similar Quaternary history to southeastern Alaska. The entire island was covered with ice except for a few nunataks and portions of the coastal plain. Further to the east, the enormous Laurentide ice sheet covered what is now northern Canada to a thickness of up to 5 km (Pielou 1991), and even today the land around Hudson Bay is rebounding at 1 cm/year (Tushingham 1992). The Fennoscandian ice sheet covered the Baltic region to a depth of 3 km (Peltier 1994); present-day uplift rates in Finland and Norway are comparable to that found for Hudson Bay. The British Isles were capped with the smaller Scotland ice sheet. Western Scotland has risen at an average of 0.16 cm/yr over the last 4000 years (Shennan & Horton 2002). Other significant ice sheets covered parts of Greenland,

Iceland, and Siberia. Smaller ice caps were present in the Southern Hemisphere in New Zealand (Newnham et al. 1999) and Patagonia (Bevis et al. 2002; Ivins & James 1999).

Isolated Fish Populations

Our objective in developing a model of Holocene uplift in southeastern Alaska was to set an upper bound on the location where isolated populations of stream-dwelling fish might be found. From the standpoint of looking for isolated populations, the search should include sites up to the highest elevation predicted by the *least* conservative model. However, in a companion paper (Hastings 2005, ch. 4), we sought to understand the factors determining persistence of isolated populations by specifically looking for sites where isolated populations had failed to persist. In that case, we used the *lowest* predicted amount of uplift as the upper bound on our search, to avoid the possibility of considering a site where fish could never have reached as a site where they had colonized but failed to persist.

Nonetheless, either uplift model supports the potential for *hundreds* of sites across southeastern Alaska where isolated fish populations may be found. These populations were all founded during the Holocene, and most would have been founded about 9,000-10,000 years ago, according to predictions about when uplift should have stabilized for most of the region (Clague et al. 1982; Mobley 1988). The rugged topography of southeastern Alaska, the many areas still largely unimpacted by the region's relatively small human population, and the plentiful availability of larger salmonids close to and in saltwater all contribute to the likelihood that many isolated populations of stream-dwelling fish have not been substantially affected by anthropogenic activities. These

populations offer an unparalleled opportunity to study the effects of isolation on small populations, particularly over longer timespans than are practical for manipulative experiments.

ACKNOWLEDGEMENTS

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Table 2.1. Highest reported elevations, by species, for isolated natural and stocked lake fish populations in southeastern Alaska. All migration barriers are directly below the lake outlets, except for Kokanee, where the lake is upstream of the barrier at 145 m (472') ASL.

Species	Origin	Elevation of Migration Barrier (ASL)
Cutthroat trout	Natural	176 m (574')
Dolly varden char	Natural	247 m (804')
Kokanee	Natural	107 m (350')
Sculpin spp.	Natural	107 m (350')
Threespine stickleback	Natural	176 m (574')
Arctic grayling	Stocked	601 m (1959')
Eastern brook trout	Stocked	952 m (3100')
Rainbow trout	Stocked	606 m (1973')

Table 2.2. Differences between uplift model for southeastern Alaska developed from geological evidence (uplifted marine sediments) and from biological evidence (isolated lake fish populations). "Low", "Medium" and "High" refer to the relative amount of post-Pleistocene uplift. Lake populations are lakes that currently contain isolated natural populations of at least one species of native fish. All elevations are ASL.

Uplift Zone	Amount of Uplift (m)	# of Lake Populations	Highest Lake Population	Mean Elevation of Lake Populations
Geological Model				
"Low"	< 30	39	140 m (458')	52 m (168')
"Medium"	30-100	36	138 m (450')	54 m (175')
"High"	100-230	38	247 m (804')	89 m (290')
Biological Model				
"Low"	< 75	25	76 m (249')	47 m (152')
"Medium"	75-140	50	140 m (458')	56 m (181')
"High"	140-245	38	247 m (804')	89 m (290')

Table 2.3. Number of sites identifed from GIS data with fish habitat isolated above upstream movement barriers, for four representative islands in the intermediate uplift zone of the central Alexander Archipelago. "Within uplift zone" refers to sites where the barrier is below the maximum predicted uplift for this area, based on the uplift model derived from biological data. Within the uplift zone, approximately one isolated site was identified for every 2000 ha of land area.

Island	Area (ha)	Isolated sites within uplift zone	Isolated sites above uplift zone
Kupreanof	279,550	139	76
Kuiu	194,654	106	74
Mitkof	54,299	23	40
Zarembo	47,580	20	29

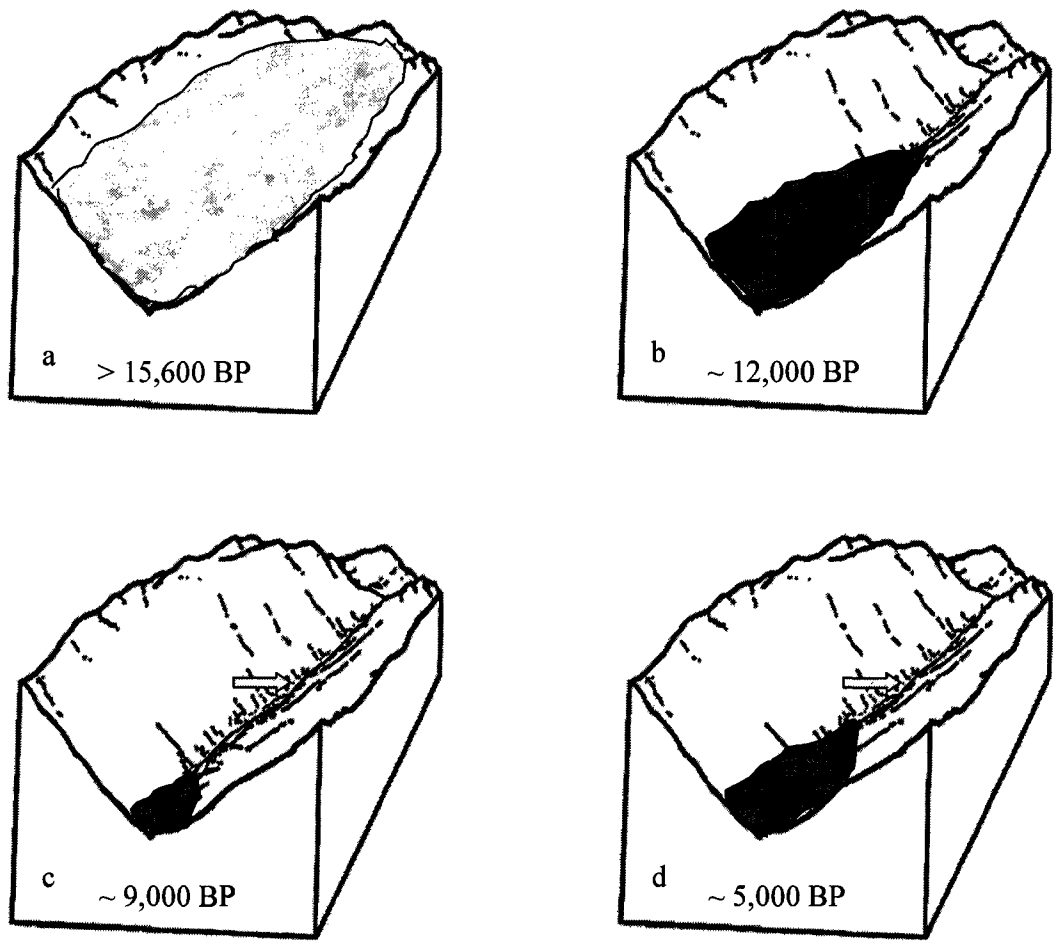

Figure 2.1. Conceptual model of population isolation due to isostatic rebound. (a) Land covered by ice sheet during Pleistocene. (b) Ice sheet retreats, exposing new streams which are quickly colonized by salmonids. (c) Land rebounds slowly from weight of ice, exposing waterfalls (arrow) that isolate upstream fish on some streams. (d) Eustatic sea level rise occurs later than rebound in southeastern Alaska.

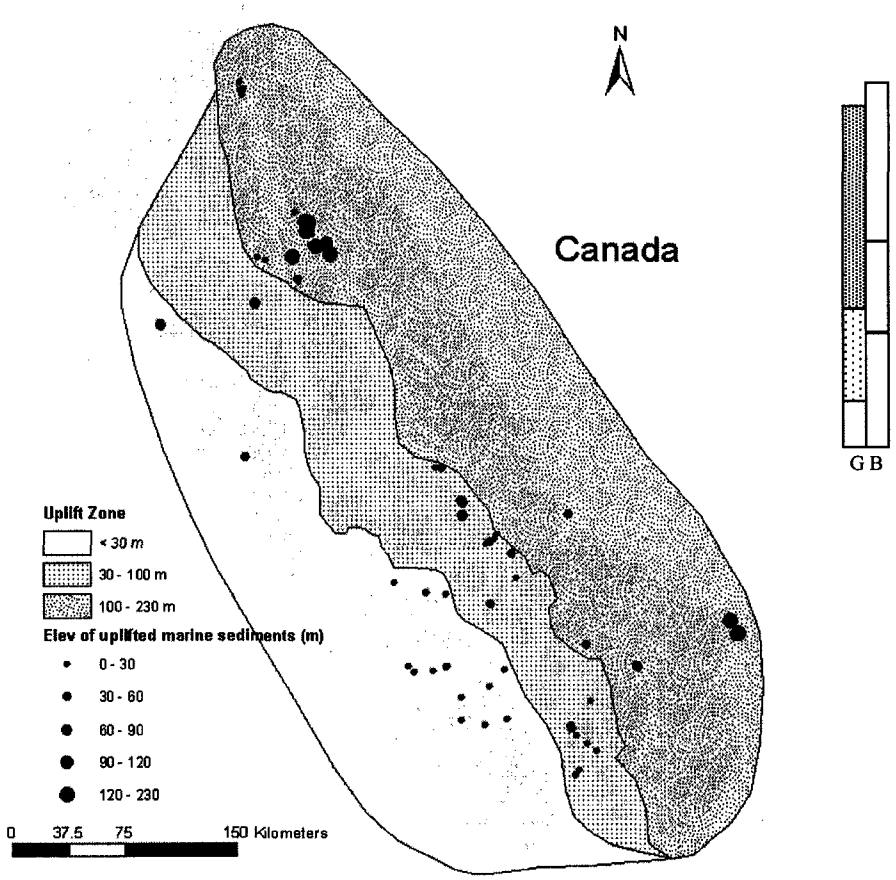

Figure 2.2. Geological uplift model for southeastern Alaska based on elevations of exposed marine sediments. Vertical bars on the ride side of the figure indicate the relative limits of the three uplift zones for the geological (shaded) and biological (unshaded) models.

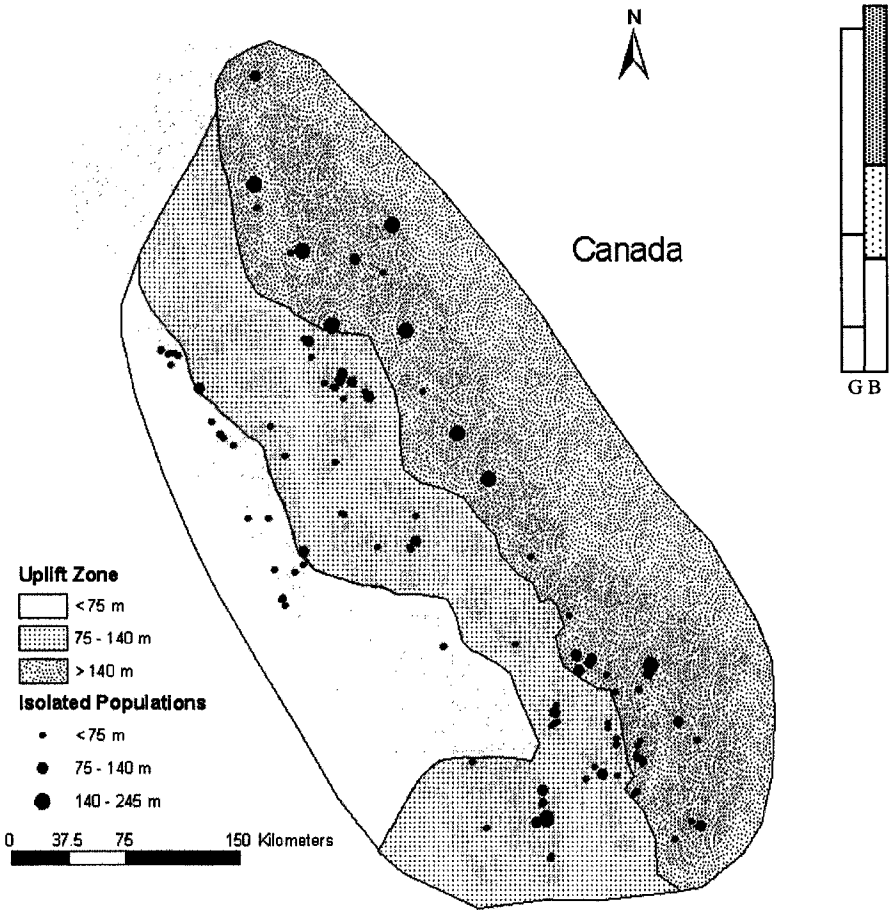

Figure 2.3. Biological uplift model for southeastern Alaska based on elevations of present-day isolated lake fish populations, showing areas shifted from the outer islands zone to inner islands zone, relative to the geological uplift model. Amount of uplift for all zones is also greater than in the geological uplift model. Vertical bars on the ride side of the figure indicate the relative limits of the three uplift zones for the geological (unshaded) and biological (shaded) models.

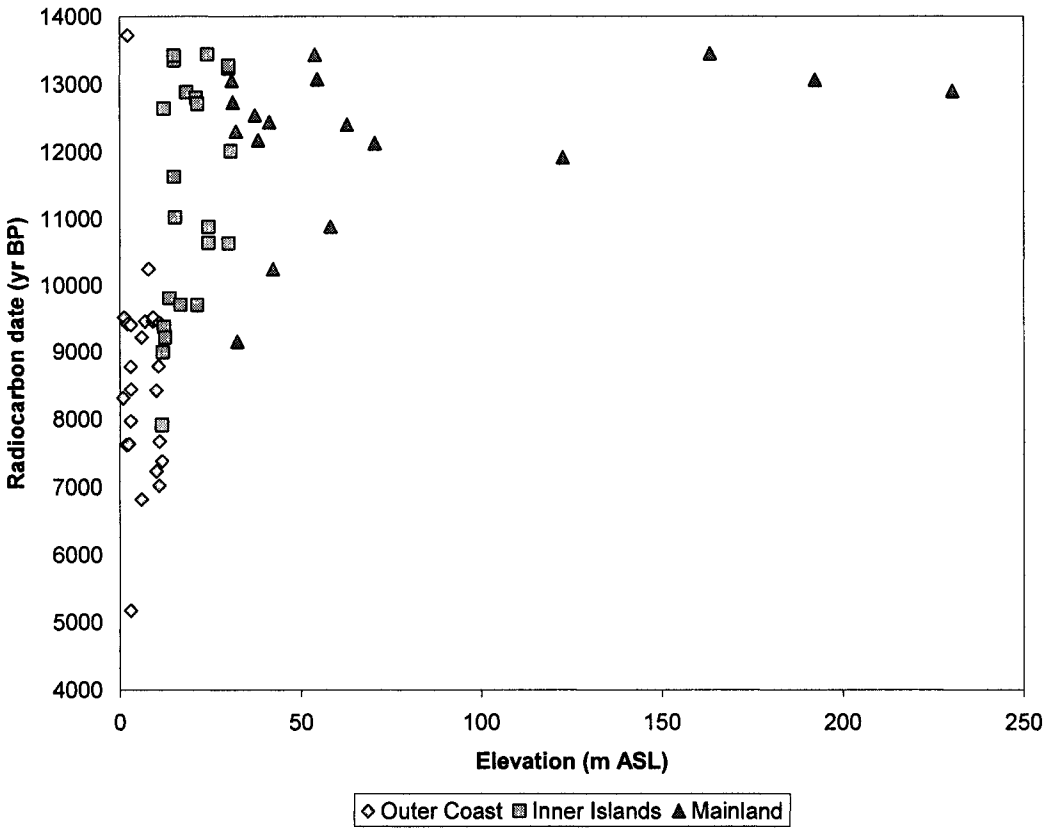

Figure 2.4. Radiocarbon dates associated with uplifted marine sediments in southeastern Alaska.

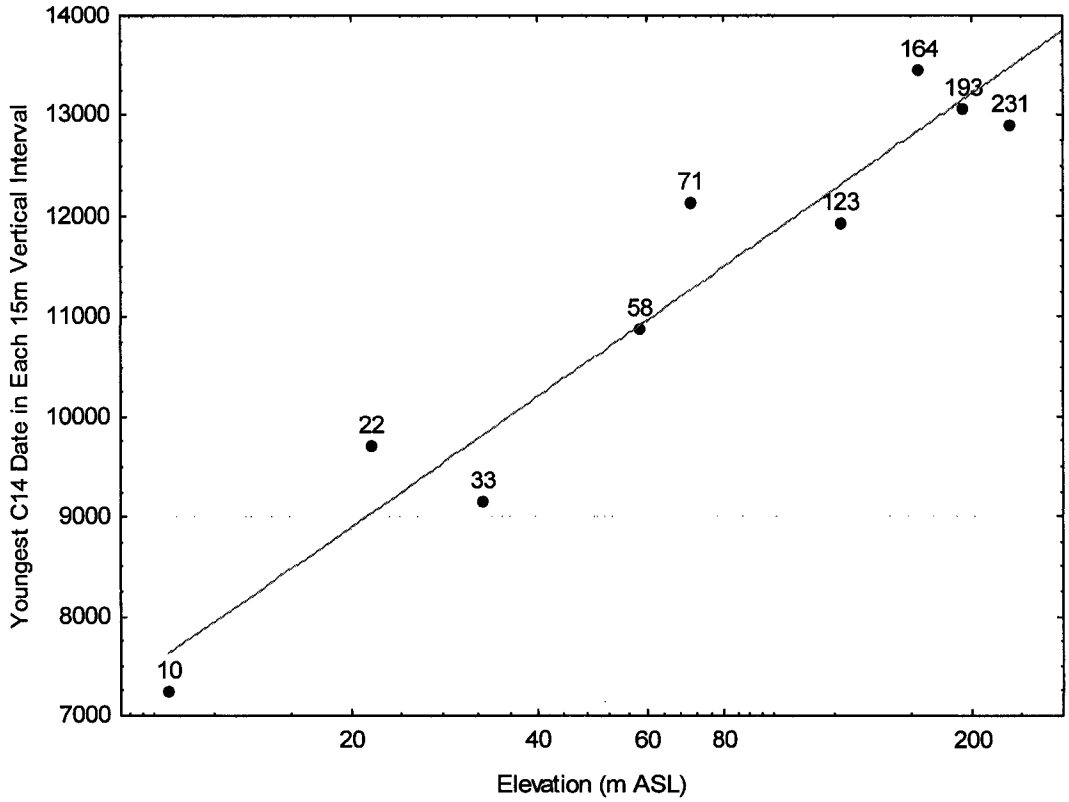

Figure 2.5. Isolation time in years related to log-transformed elevation (r^2=0.92; $p < 0.001$). Point labels are elevation in meters ASL. Isolation times are the ages of the youngest known uplifted marine sediments from each 15m vertical elevation stratum regionwide.

CHAPTER 3 – Genetic Diversity of Naturally Isolated Populations of Coastal Cutthroat Trout (*Oncorhynchus clarki clarki*)

ABSTRACT

Small populations are threatened by a variety of genetic, demographic, and environmental factors, but few studies have examined the relationships between these factors. We studied populations of coastal cutthroat trout (*Oncorhynchus clarki clarki*) to explore the interaction of these factors through ecological time, and their effects on small, naturally isolated populations. We sampled fish from above and below migration barriers (waterfalls) exposed by isostatic rebound on 12 streams in southeastern Alaska. We examined eight microsatellite loci to investigate genetic variability within and among collections above and below the barriers. All of the above-barrier populations showed greatly reduced heterozygosity and allelic diversity when compared to any of the below-barrier collections. Furthermore, the amount of genetic diversity retained by isolated populations was highly correlated with the amount of habitat available. For the above-barrier populations, we calculated effective population size from the reduction in heterozygosity observed, and compared this "genetic" population estimate with "demographic" population size estimates calculated from the amount of above-waterfall habitat. Estimates of effective population size were higher than what would be expected from the amount of habitat, but this may have been due to uncertainties in the data. Our results suggest that the amount of habitat available to a population is a key determinant of population persistence, not only for demographic reasons but for genetic ones as well.

INTRODUCTION

Much of conservation biology deals with assessing and maintaining the viability of small populations. What Caughley (1994) termed the "small population paradigm" classifies the threats to the persistence of small populations into three categories: genetic, demographic, and environmental. While debate has raged over which of these categories is the more important, few studies have examined the relationships between them.

One reason for this deficiency is that completely isolated natural populations are hard to find. We know that even a single migrant per generation can be sufficient to forestall the loss of genetic variation (Mills & Allendorf 1996) and its deleterious effects (Newman & Tallmon 2001). Studies of apparently isolated populations of terrestrial vertebrates have frequently found that there is greater dispersal and consequently much less differentiation between populations than expected (*e.g.* Funk 2004; Tallmon 2001). Isolated populations can be created in the laboratory (Montgomery et al. 2000), but their responses lack the complexity of those in natural settings.

Freshwater fish provide some of the best examples of naturally isolated populations. Bedrock waterfalls that eliminate the possibility of upstream migration isolate the populations above them from the rescue effect of immigrants (*sensu* Brown & Kodric-Brown 1977). A number of studies have demonstrated that such isolated fish populations are genetically differentiated from those downstream (Carlsson & Nilsson 2001; Castric et al. 2001; Costello et al. 2003; Currens et al. 1990; McGlashan & Hughes 2000). We studied genetic and demographic characteristics of small, isolated populations of coastal cutthroat trout (*Oncorhynchus clarki clarki*) in southeastern Alaska. Many such populations, sometimes alone and sometimes sympatric with Dolly Varden

(*Salvelinus malma*), have been isolated by uplift for thousands of years in this highly fragmented landscape, providing an unusual opportunity for replicated studies.

Our broad goal was to explore the interactions between genetic and demographic factors that threaten the persistence of small populations, using coastal cutthroat trout populations above and below permanent, upstream movement barriers. Our first objective was to use patterns of genetic variation to determine whether the above-barrier populations were indeed reproductively isolated. Second, for small populations that have been reproductively isolated for many generations, we tested whether the amount of genetic variation lost was correlated with population size and with length of isolation period. Finally, we examined whether the quantitative loss in genetic variation was similar to what we would expect for isolated populations.

MATERIALS AND METHODS

Area and Populations of Study

The Alexander Archipelago is a long chain of islands that hug the coastline of the southeastern Alaskan panhandle between 54°40' N and 58°30' N. The archipelago covers approximately 500 km of latitude and 150 km of longitude, and it includes, by one estimate, over 22,000 islands (USDA Forest Service 1997). It is rugged, naturally fragmented terrain, partitioned by many steep-sided mountain ranges and deep, saltwater fjords. Compared to continental watersheds elsewhere in North America, the numerous island watersheds in the Alexander Archipelago are quite small. The longest island stream is only about 30 km long, excluding tributaries, and the majority of streams are less than 10 km in total length.

During the Pleistocene, the Archipelago and the adjacent continental coast were almost totally covered with ice (Mann 1986), unlike the Beringian and Cascadian refugia to the north and south, respectively. It is unlikely that freshwater refugia were available to fish anywhere in southeastern Alaska. Late Pleistocene ice retreat in the region was largely complete by about 12,500 BP (Mann 1986), exposing many new streams for colonization from saltwater. Research on recently deglaciated streams in Glacier Bay (Milner & Bailey 1989; Milner et al. 2000) suggests that the lower reaches of such streams would nearly all have been colonized by anadromous salmonid fishes early in the Holocene. About half of the approximately 72,000 km of mapped streams in southeastern Alaska are presently considered fish-bearing (USDA Forest Service 1997), and most fish species present are widely distributed throughout the region (Morrow 1980). In the first few millennia following the retreat of the Cordilleran icesheet, isostatic rebound exposed geological discontinuities in the bed of many streams. These exposed waterfalls permanently blocked any upstream migration, and created isolated populations upstream.

We selected 12 streams in central southeastern Alaska with populations of coastal cutthroat trout upstream of permanent movement barriers (Figure 3.1). We generally avoided populations that had access to a lake upstream of the barrier because we wanted to focus on the smallest natural populations we could find Strictly stream-dwelling populations are likely to be much smaller than lake-dwelling populations. Also, lakes are more likely than streams to have experienced stocking or other forms of anthropogenic supplementation. The amount of above-waterfall habitat available to our stream-resident populations ranged from 1 to 28 km (Table 3.1). Bankfull width was typically about 5 m.

In some cases, coastal cutthroat trout were the only fish found in the above-barrier portion of a stream, while in others, Dolly Varden were also present.

Sample Collection

We collected fin clips from coastal cutthroat trout below and above upstream movement barriers on eight streams. We collected above-barrier samples from a further four streams where we were unable to obtain satisfactory below-barrier samples, yielding a total of 12 above-barrier collections and eight corresponding below-barrier collections (Table 3.1; Figure 3.2). Of the four streams lacking comparable below-barrier collections, three were compromised by hybridization with rainbow trout (*O. mykiss*). At the fourth site (Leprechaun), we were simply unable to capture enough coastal cutthroat trout, despite making multiple attempts using a wide variety of sampling methods.

Approximately 30 fish at each site were captured using minnow traps, electroshocking, or hook and line. Fish were temporarily anesthetized using MS-222 or clove oil (Woody et al. 2002). A non-lethal fin clip (less than 0.25 cm^2) was removed from the dorsal or anal fin (rarely, the adipose fin). Fin clips were stored at room temperature in 95% ethanol.

Overall, sample streams were chosen to represent a gradient in amount of above-barrier habitat, ranging from small drainages that were apparently barely sufficient to support an isolated population, to drainages at least an order of magnitude larger in size. Fish from below barriers were sampled as close to saltwater as possible to increase the likelihood of sampling anadromous fish that would presumably be parted of a larger regional population or metapopulation, or at least those freshwater-resident fish that were

most likely to have recently exchanged genetic material with anadromous fish. Above barriers, we sampled fish throughout their available habitat in the smaller drainages, and at a centrally situated and apparently representative site in the larger drainages.

Microsatellite amplification and allele scoring

DNA was extracted using the Pure Gene® kit from Gentra following the manufacturer's instructions. Fin clips were removed from the ethanol and placed directly in the Gentra "cell lysis solution" to which 3 µl/600 ml protease (SIGMA) had been added. We amplified eight microsatellite loci in an MJ Research PTC-200 thermocycler (Table 3.2). Amplified products were size fractionated on 7% denaturing polyacrylimide gels and visualized using a Hitachi FMBIO-II flourescent imager. Product sizes were determined using MapMarkerLOW™ size standards (Bio Ventures Inc.) and Hitachi FMBIO software (version 8.0). Each gel also included previously amplified individuals to ensure consistent scoring across all gels. We developed three-locus multiplex sets for six of the loci, following the methods of Wenburg et al. (1996). The remaining two loci were amplified separately (Table 3.2).

All eight microsatellite loci were polymorphic in southeastern Alaskan coastal cutthroat trout (Table 3.2). One of our loci (*Ocl3*) had been previously published (Condrey & Bentzen 1998) as two independent loci (*Ocl3* and *Ocl4*), but these are actually the same locus (*i.e.* the *Ocl3* F primer aligns 72 bp further out on the template DNA than the *Ocl4* F primer; confirmed by P. Bentzen, *pers. comm.*). We found *Ocl3* to be the easier of the two to score.

Hybridization with Rainbow Trout

We screened all coastal cutthroat trout samples from below-barrier populations for evidence of hybridization with rainbow trout, using genetic markers derived from paired interspersed nuclear elements (PINEs, Spruell et al. 2001). We also randomly selected 10 fish from each above-barrier to screen for evidence of hybridization. PINE PCR conditions, electrophoresis details, and methods for scoring amplification products followed those described by Spruell *et al* (2001). We identified hybrids using four previously developed PINE markers (Hpa1 5' / Hpa1 3': 66bp and 70 bp; and Hpa1 5' / 33.6+2: 266 bp and 395 bp) shown to be diagnostic between rainbow trout and coastal cutthroat trout (Hitt et al. 2003; Kanda et al. 2002).

We detected evidence of hybridization between coastal cutthroat trout and rainbow trout in 3 of 11 below-barrier populations (Mason, Portage, and Hiller). In the populations where hybrids were detected, rainbow trout markers were common, despite our attempts to use visual characteristics (color of hyoid slash, length of maxillary extension) to exclude rainbow trout from our field samples. All three below-barrier populations showing evidence of hybridization were excluded from our analysis. No evidence of hybridization between rainbow and coastal cutthroat trout was detected in any of our above-barrier populations.

Genetic Data Analysis

We used the computer program FSTAT version 2.9.3 (Goudet 2001) to test for significant allele frequency differences among all pairwise comparisons using the log-likelihood statistic G, and to screen for: (1) departures from Hardy-Weinberg proportions

for each locus-population combination; (2) genotypic linkage disequilibrium between all pairs of loci within each population and for all populations pooled. Where required, the threshold for statistical significance ($\alpha = 0.05$) was adjusted for k simultaneous tests using the sequential Bonferroni method (α/k;(Rice 1989)). We also used FSTAT to calculate genotypic variation (allelic richness and expected heterozygosity) at each locus, for each population, and over all loci among all populations.

To explore population divergence, we calculated estimates of F_{ST} and F_{IS} with FSTAT, using the "weighted" analogues θ_{ST} and θ_{IS} (Weir & Cockerham 1984). We looked at: (1) the divergence among the saltwater-connected, below-barrier populations, which are capable of exchanging migrants from time to time; (2) the divergence among the isolated, above-barrier populations; and (3) the average divergence between above- and below-barrier pairs in each stream. To estimate above-below divergence for the four unpaired above-barrier samples, we averaged the values of the divergence statistic between that above-barrier sample and each of the eight below-barrier samples.

An analysis of molecular variation (AMOVA; Michalakis and Excoffier 1996) was also conducted to further explore genetic population structure. AMOVA was performed using ARLEQUIN version 2.000 (Schneider et al. 2000). We contrasted the partitioning of variation among above-barrier populations, among below-barrier populations, and among above-below pairs in the same stream. Randomization tests were used to test whether F-statistics were significantly greater than zero.

We used STATISTICA version 6.0 (Statsoft 2001) to perform a principal components analysis of allele frequencies, using the covariance method. The largest allele at each locus was omitted to account for the non-independence of allele frequencies

within a locus (Cavalli-Sforza et al 1993). STATISTICA was also used for all correlation and regression analyses.

Effective Population Size Estimated From Genetic Data

We calculated effective population size (N_e) from the loss in heterozygosity over time (Crow & Kimura 1970):

$$N_e = \frac{1}{2(1-e^a)} \quad (1)$$

where

$$a = \frac{\ln\left(\frac{H_t}{H_o}\right)}{t} \quad (2)$$

H_o is the initial heterozygosity and H_t is the heterozygosity at generation t. We estimated H_o, the presumed heterozygosity of the common founding population for all above-barrier populations, as the average of H_e for all present below-barrier populations. For the first set of N_e estimates, we compared H_e for each above-barrier population with this estimated H_o.

To determine the total amount of time since the populations were founded, we turned to recent geological evidence. We used radiocarbon dates for shell fragments from exposed, uplifted glaciomarine sediments to establish the earliest time that land at different elevations could have emerged from saltwater. From a larger dataset of 65

radiocarbon-dated, exposed glaciomarine sediments, we selected the most recent date found in each 15 m vertical elevation band and regressed it on log-transformed elevation to produce a formula for predicting the time that a given elevation emerged from the sea during Holocene uplift (Figure 3.3; for more details see Hastings 2005, chapter 2).

We considered mean generation interval to be 3 years, since what little published evidence is available suggests that these fish spawn from age 2 to age 4 (June 1981, Nicholas 1978, Wyatt 1959). To estimate t for each isolated stream reach, we divided the estimated number of years since the elevation at the top of the barrier had emerged from saltwater by the estimated generation time for these fish.

Population Size Estimated From Demographic Data

We estimated adult population size (N) for each sampled stream by multiplying average above-barrier adult fish density (adult fish/stream length) by the length of stream habitat above the barrier. We estimated the length of above-barrier habitat using the spatial database (GIS) of streams maintained by the Tongass National Forest (TNF). We summed the length (to the nearest 0.1 km) of all contiguous stream segments above the barrier that are of channel types considered to be fish-bearing (Paustian et al 1992). This was possible because all stream segments in the TNF GIS database have been channel-typed from aerial photographs, to a 0.1 km resolution. Accuracy of stream channel typing solely from photo interpretation is about 75% (S. Paustian, *pers. comm.*). However, the accuracy of binary assignment to fish-bearing *vs.* non fish-bearing channel types is much higher. As well, ground-truthing has improved data quality to an unspecified degree for some parts of the original streams database. We then applied a

multiplier to account for the fact that GIS-mapped habitat was less than the total amount of habitat in any system. The TNF GIS did not originally map stream segments that could not be inferred from aerial photographs, generally leaving out the smallest tributaries, and in addition GIS-mapped stream segment lengths are generally shorter than actual stream length because not every twist and turn is captured by the digitized stream representations in the GIS. To estimate the ratio of actual habitat to GIS-mapped habitat for our streams, we formally ground-truthed the total amount of habitat at one of our sites (Leprechaun) and informally estimated it at several others.

To determine average above-barrier adult fish density, we sampled the entire length of a single above-barrier stream (also Leprechaun). Fifty-meter reaches were consecutively sampled with baited minnow traps over a 12 day period in late summer 2001, using a three-pass removal sampling design (Bryant 2000). We used Program CAPTURE (Rexstad & Burnham 1991; White et al. 1978) to generate an abundance estimate for the entire stream, summing the captures for each pass along the full length of the stream. We then divided the abundance estimate by the length of the stream to arrive at an estimate of density in terms of stream length (fish/m).

This whole-stream density estimate (Table 3.3) was compared with similarly derived point estimates taken from above-barrier reaches (mean length 125 m) in 23 streams sampled annually by TNF for 1-5 years (USFS 2003, pp. 2-18, and unpublished TNF data for 2003 and 2). TNF chose to sample reaches with high quality habitat, so these density estimates were likely somewhat higher than densities in other stream channel types. We used the TNF estimates to evaluate whether our whole-stream density

estimate was broadly representative of fish in similar settings, especially isolated stream reaches that did and did not contain sympatric populations of Dolly Varden char.

We chose to express fish density in terms of stream length rather than stream area, because measurements of stream length are more easily obtained than stream area. Estimated stream length was available for all streams in this study, but stream area was not. However, because we did know stream area for each of the reaches where fish density was sampled, for those reaches we compared density per area and per length, to test whether our choice to express fish density in terms of stream length would introduce a bias relative to density per stream area, for streams of this size.

RESULTS

Genetic Variation Within Populations

Tests for deviation from Hardy-Weinberg proportions were significant in 13 of 160 (8%) cases ($\alpha = 0.05$), distributed across 7 of 8 loci and 9 of 20 populations. Most of these cases (9 of 11) were heterozygote deficits. When α was adjusted for multiple comparisons ($\alpha = 0.0025$ for simultaneous tests on 20 populations, or $\alpha = 0.00625$ for simultaneous tests on 8 loci), significant heterozygote deficits were found in only 3 or 4 of 160 cases, respectively. No one locus displayed consistent deviations from Hardy-Weinberg proportions, but one below-barrier population in particular (RGB) exhibited significant heterozygote deficits at 4 loci (2 when α was adjusted for multiple comparisons), as well as non-significant heterozygote deficits at all of the remaining loci.

Tests for genotypic linkage disequilibrium for each of 28 possible locus pairs in each population (n=20) were significant in 10 of 560 (2%) pairwise comparisons (initial α

= 0.05, adjusted to 0.0018 for 28 simultaneous tests in each population). Again, eight of the ten significant combinations were found in the below-barrier RGB sample. These locus combinations were not the same as the significant locus combinations found for the remaining two populations. The most likely explanation for the deviation from Hardy-Weinberg proportions and the linkage disequilibrium observed in the RGB sample is that above-barrier fish emigrating over the barrier falls influenced the genetic makeup of the below-barrier sample.

Each of the above-barrier populations exhibited lower genetic diversity than any below-barrier population, in all cases and by all measures (Table 3.4, Figure 3.4). For the below-barrier populations (n = 8), average number of alleles per locus ranged from 3 (*Oneu11*) to 8 (*Omy77*). Allelic richness in below-barrier populations averaged 4.80 across all populations and all loci. For the individual above-barrier populations (n = 12), average number of alleles per locus ranged from 2 (*Oneu11, Ocl2, Ogo8,* and *Ocl1*) to 3 (*Sfo8, Omy77,Ogo4,* and *Ocl4*), and allelic richness averaged 2.32 across all populations and all loci. Expected heterozygosities averaged across below-barrier populations for each locus ranged from 0.25 (*Oneu11*) to 0.77 (*Omy77*) and, overall, averaged 0.62. Expected heterozygosities averaged across above-barrier populations for each locus ranged from 0.19 (*Oneu11*) to 0.44 (*Omy77*) and, overall, averaged 0.32.

Genetic Divergence Among Populations

Significant allele frequency differences were detected among all pairwise comparisons for the 20 population samples at each locus and over all eight loci ($p <$ 0.0001). F_{ST} among below-barrier populations was 0.099, similar to what Wenburg et al.

(1998) found in anadromous coastal cutthroat trout populations in western Washington state. However, among the isolated, above-barrier populations F_{ST} was much greater (0.570). AMOVA produced identical values for F_{ST}, and showed that for the below-barrier populations, most of the genetic variation (90%) is found within populations (Table 3.5). For the above-barrier sites, however, there was greater variation among populations than within (57% *vs.* 43%). All measures of genetic differentiation were significant ($p < 0.00001$). When populations in the same stream were grouped together (above *vs.* below), estimates of between-stream ($F_{CT} = 0.105$) differentiation were less than differentiation within stream pairs ($F_{SC} = 0.287$). That is, differentiation between the above- and below-barrier populations in the same stream was pronounced (Figure 3.5), even when compared to the differentiation between any two stream "groups" (a group in this case being the above-below pair for a single stream)..

We conducted a principal components analysis (PCA) of allele frequencies to examine patterns of genetic similarity, (Figure 3.6). As would be expected given the relatively low below-barrier F_{ST}, all of the below-barrier populations are tightly clustered together in the PCA. On the other hand, the above-barrier populations are more loosely distributed in an apparently random fashion around the central cluster. This pattern of genetic variation is consistent with the expectation that genetic drift is driving the above-barrier populations apart, while limited gene flow is maintaining a degree of homogeneity in the below-barrier populations.

Correlation between Genetic and Demographic Characteristics of Isolated Populations

Both measures of within-population genetic variation (expected heterozygosity and allelic richness) were strongly correlated with the log-transformed amount of habitat available to an above-barrier population (Figures 3.7a and 3.7b). The more space available to an isolated population, the greater was its retained genetic variation. These results were not surprising, since habitat length should correspond approximately to population size, which is a key determinant of maintenance of genetic variation in an isolated population.

The other factor that determines loss of genetic variation over time in an isolated population is the length of the period of isolation. We examined the residuals from each of the above habitat length regressions for correlation with isolation period, but no significant pattern was found.

When we directly compared estimates of effective population size from genetic and from environmental data, the correlation is strong (Figure 3.8). However, while the two estimates are of the same order of magnitude for the majority of our streams, they are clearly not identical for most streams nor overall (in other words, the slope of the correlation line is 1.6, rather than 1, and the intercept is at ~1250, rather than 0).

Estimated N_e/N ratios varied among our streams from as low as 0.17 to as high as 4.03 (Table 3.6). We found that the exceptionally high N_e/N ratios were all associated with our smaller populations (Figure 3.9). When the three outlier ratios greater than 1.0 were removed, the average estimated N_e/N we observed was 0.41, about twice what has been suggested for adult salmonids in general (Allendorf et al. 1997).

DISCUSSION

Above-Barrier Populations Are Isolated

One of our fundamental objectives was to identify a set of isolated populations in which we could study the long-term effects of isolation. We demonstrated a consistent pattern of dramatically reduced genetic variation in our above-barrier populations, which would be highly unlikely if any of the above-barrier populations were exchanging genetic material with any other population. These results provide strong support for our assumption that the above-barrier populations have been completely, or at least largely, isolated, since it would take only an occasional immigrant to maintain gene flow among populations (Mills & Allendorf 1996).

The pattern of independent genetic drift exhibited by the set of above-barrier populations provides further support for this conclusion. If even a small amount of gene flow were occurring between the individual populations, at least some of the populations would tend to resemble others. Instead, the populations that stand out do so because they look less like the others, not more.

Genetic Variation is Strongly Correlated with Habitat Size

We found genetic variation to be highly correlated with habitat amount for our above-barrier populations. Correlations between genetic variation and population size were reviewed by Frankham (1996), who found highly significant correlations across many taxa. Frankham (1996) tested correlation between genetic variation and a number of correlates of population size, including island size or "habitat island size," and found genetic variation to be well correlated with the amount of available habitat, as we did.

Frankham's (1996) conclusions and our results confirm early observations by Soule (1976), a result predicted by population genetics theory (Wright 1969).

We were unsuccessful in detecting the direct influence of isolation period on genetic variation, although this relationship is also predicted by population genetics theory. The most likely explanation for why we were unable to detect the influence of isolation period was that all of our above-barrier populations have been isolated for very long periods. Because genetic variation decays exponentially with time, the differential influence of isolation period will be most pronounced early in the isolation process. For example, with an effective population size of 500 breeding adults, two-thirds of the initial genetic variation will, on average, be lost within 1000 generations. The populations we studied have been isolated 3 to 4 times longer than that, to a point where less than 95% of the initial genetic variation is expected to remain. The number of populations we sampled may simply not provide the power to detect small differences in the influence of isolation period after that length of time, particularly as our populations span more than an order of magnitude difference in the amount of habitat available.

Quantitative Loss of Genetic Variation Over Time May Be Less Than Expected

While the correlation between genetic variation and the amount of habitat available to our isolated populations was high, the quantitative loss in genetic variation that we observed was less that what would be suggested from the amount of habitat. One way to compare the two estimates is to examine the ratio of effective population size to census population size (N_e/N). Frankham (1995b) reviewed 192 published estimates of N_e/N in 102 species and found the average to be 0.11. In contrast, we observed a mean

N_e/N of 1.01. The median N_e/N we observed, which discounts the importance of a few very high estimates, was 0.43. In other words, our isolated populations "acted" larger, in terms of retaining genetic variation, than they appeared to be. Although N_e/N ratios may actually have been this high in our populations, it is more likely that our estimated ratios of N_e/N were biased by uncertainties in the parameters that went into them, especially those that were estimated rather than measured.

Our estimates of N_e depended on measured heterozygosities, and on estimated generation time and period of isolation. We estimated the length of time populations have been isolated from patterns of isostatic rebound (Hastings 2005, chapter 2). Because regional variation in uplift was undoubtedly more complex than we were able to map from the available evidence, there is certainly some question about the exact time we assigned for emergence of each individual stream from saltwater, but there is no reason to expect a consistent bias overall. On the other hand, generation time has not been measured for stream-resident coastal cutthroat trout and our estimate of 3 years per generation may have been low. While other studies have found that coastal cutthroat trout in similar settings rarely live longer than 4 years (June 1981; Wyatt 1959), new data from southeastern Alaska suggest that fish in these settings may live for 10 years or more (K. Hastings, unpublished data). Were this the case, our estimates of generation time would be lengthened and hence the number of generations spent in isolation reduced. Consequently, we would expect less loss of genetic variation and a larger estimate of N_e. The proportional increase in N_e would be identical to the proportional increase in generation time, so for most of our isolated populations a generation time of 6 years

would result in N_e/N ratios that are in accordance with what others have found. For this and other reasons, we plan to further investigate the age structure of these populations.

Our estimates of census population size (N) depended on measurements of habitat length and estimated fish density. In the shortest streams, we completely measured all available habitat, ruling out the possibility of substantial inaccuracies in habitat length. For larger drainages, where habitat length was measured using GIS data derived from aerial photo interpretation, any bias would most likely be towards underestimating true habitat length, since photointerpretation in forested settings tends to miss smaller channels, and since maps of stream channels tend to smooth out and shorten the twists and turns that the actual channel takes, a fractal effect. Were such a bias present, we would have seen a positive correlation between N_e/N and habitat length, but no such correlation was observed.

The confidence interval on our fish density estimates from a wide variety of streams was quite narrow, and the estimates are similar to those for trout populations in headwater streams elsewhere (Hilderbrand & Kershner 2000). However, in the early Holocene when stream environments in the region were less hospitable, it is possible that fish densities may have been lower. If that were the case, we may have overestimated N for part of the isolation period, but this would bias N_e/N ratios low, not high.

A higher than predicted N_e/N can result when selection prevents a population from losing genetic variation at the rate predicted by Wright (1969). Also, our isolated coastal cutthroat populations are likely to be less fecund than anadromous salmonids, which could translate to relatively small fluctuations in population size and relatively large N_e/N ratios when compared to salmonids as a group (Kalinowski & Waples 2002;

Vucetich et al. 1997; Waples 2002). Other factors that can affect N_e/N include unequal sex ratios and variance in family sizes (Frankham 1995b). All of these, however, act to reduce, not increase, N_e/N.

Negative Correlation Between N_e/N and N

We observed a pattern of decreasing N_e/N ratio with increasing census population size (N). In other words, small populations appear to retain proportionately greater genetic variation than large populations. This pattern has also been reported in a few other species, according to several studies reviewed by Frankham (1995a; 1995b). These include *Drosophila* (Nozawa 1963, 1970), the red flour beetle *Tribolium castaneum* (Pray et al. 1996; Wade 1980), the moth *Panaxia dominula* (Wright 1969), and the plant *Eichornia paniculata* (Husband & Barrett 1992). As Kalinowski and Waples (2002) have pointed out, this phenomenon deserves further investigation as it may influence the rate of genetic drift during population bottlenecks.

CONCLUSIONS

We identified a set of naturally isolated small populations ideal for exploring the predictions of the small population paradigm. Stream-resident coastal cutthroat trout above waterfalls in southeastern Alaska display greatly reduced genetic variation and adult population sizes as small as a few thousand individuals, yet at least some have managed to persist for thousands of generations. The correlation between genetic variation and habitat size in these populations is very high, underscoring the importance of reserve size in the preservation of small populations.

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Table 3.1. Sites where coastal cutthroat trout tissue samples were collected. rainbow trout alleles were detected, the number of fish with rainbow trout alleles is also given in parentheses. "Habitat above" is the length of fish habitat above the barrier. Isolation is the approximate length of time the population is believed to have been isolated, based on the elevation of the top of the barrier.

Site Name		Site Code	Sample Size	Habitat Above (m)	Barrier Elevation (m ASL)	Isolation (yrs BP)
Duncan	Above	DNA	30	5,700	100	12,000
"	Below	DNB	33	--	--	--
Dry Straits	Above	DSA	27	7,800	15	8,500
"	Below	DSB	21	--	--	--
Jenkins	Above	JEA	30	1,400	130	12,500
"	Below	JEB	29	--	--	--
McHenry's	Above	MHA	22	1,500	52	10,500
"	Below	MHB	26	--	--	--
North Arm	Above	NAA	29	28,800	15	8,500
"	Below	NAB	29	--	--	--
Rugby	Above	RGA	29	3,900	14	8,000
"	Below	RGB	20	--	--	--
Whitecap	Above	WCA	27	1,600	81	11,500
"	Below	WCB	31	--	--	--
West Fools	Above	WFA	30	14,100	58	11,000
"	Below	WFB	30	--	--	--
Hiller	Above	HLA	20	20,000	38	10,000
"	Below*	HLB	25 (14)	--	--	--
Leprechaun	Above	LPA	30	2,000	138	12,500
Mason	Above	MAA	29	9,100	61	11,000
"	Below*	MAB	40 (22)	--	--	--
Portage	Above	POA	30	12,700	89	11,500
"	Below*	POB	30 (11)	--	--	--

*Dropped from analysis because of presence of hybridization

Table 3.2 Summary of microsatellite loci screened. Number of alleles and allele size ranges are for entire data set (N = 604). PCR details are provided for new multiplex sets developed in this study.

Locus	Number of alleles	Allele size range (bp)	Primer concentration (μM)	Annealing temperature (°C)	Reference
Sfo8[1]	14	188-236	0.375	56	Angers et al. 1995
Omy77[1]	19	102-142	0.450	56	Morris et al. 1996
Oneu11[1]	4	142-146	0.225	56	Scribner et al. 1996
Ogo4[2]	13	120-152	0.375	58	Olsen et al. 1998
Ogo8[2]	5	92-100	0.375	58	Olsen et al. 1998
Ocl2[2]	13	116-158	0.375	58	Condrey and Bentzen 1998
Ocl1	5	140-156	0.375	60	Condrey and Bentzen 1998
Ocl3 / *Ocl4*	11	58-90	0.375	55	Condrey and Bentzen 1998

[1]First multiplex set
[2]Second multiplex set

Table 3.3. Adult coastal cutthroat trout (CCT) density estimates for 17 above-barrier headwater streams, derived from 3-pass removal sampling. Density estimates are expressed in fish/linear m of stream habitat. DV = Dolly Varden char also present. Portions of USFS streams (80-227m per stream) were repeat sampled in "good" habitat from 1 to 5 times annually 1999-2003. Leprechaun Creek (LPA) was sampled continuously though its entire 2 km above-barrier section on a single occasion in 2001.

Source of data	n Streams	n Samples	Mean CCT density	Minimum CCT density	Maximum CCT density
USFS (all CCT streams)	16	64	0.46 +/- 0.07	0.01	1.22
USFS (CCT/DV streams)	12	45	0.47 +/- 0.09	0.01	1.22
USFS (CCT-only streams)	4	19	0.42 +/- 0.08	0.21	0.82
LPA (all habitat - 2150m)	1	1	0.35 +/- 0.01	--	--
LPA ("good" habitat only - 850 m)	1	1	0.40 +/- 0.02	--	--
LPA ("poor" habitat only – 1300 m)	1	1	0.32 +/- 0.02	--	--

Table 3.4. Genetic variation within above- and below-barrier populations. Heterozygosities and number of alleles reported for "all populations" are averages for the respective set of populations. Losses in He and allelic richness for each above-barrier population are as compared to the means for all below populations pooled.

	Mean He above	Mean He below	Mean He lost above	Allelic richness above	Allelic richness below	Mean allelic richness lost above
DNA / DNB	0.500	0.609	19%	3.38	4.69	30%
DSA / DSB	0.454	0.598	26%	2.83	4.90	41%
JEA / JEB	0.396	0.658	36%	2.37	5.54	51%
MHA / MHB	0.169	0.555	73%	1.46	3.94	70%
NAA / NAB	0.503	0.604	18%	3.62	4.74	25%
RGA / RGB	0.264	0.668	57%	1.74	4.54	64%
WCA / WCB	0.000	0.611	100%	1.00	4.88	79%
WFA / WFB	0.206	0.625	67%	1.84	5.18	62%
HLA	0.405	--	34%	3.06	--	36%
LPA	0.305	--	50%	1.96	--	59%
MAA	0.264	--	57%	2.03	--	58%
POA	0.345	--	44%	2.59	--	46%
All pops	0.318	0.616	48%	2.32	4.80	52%

Table 3.5. Hierarchical gene diversity analysis of 20 coastal cutthroat trout populations. When samples were grouped by stream, only streams with both above- and below-barrier samples were included. Asterisk (*) denotes $P < 0.00001$ that the value of the F-statistic is not greater than zero. CT = between streams; SC = within streams.

Grouping Strategy	Source of Variation	σ^2	Percent of Total	F_{ST}	F_{CT}	F_{SC}
Below only (8 populations)	Total	2.347	100.00			
	Within populations	2.114	90.07			
	Among populations	0.233	9.93	0.099*		
Above only (12 populations)	Total	2.503	100.00			
	Within populations	1.077	43.03			
	Among populations	1.426	56.97	0.570*		
By stream (paired streams only -- 8 groups)	Total	2.485	100.00			
	Within populations	1.586	63.82			
	Among populations	0.899	36.18	0.362*		
	Among streams	0.262	10.54		0.105*	
	Between populations in the same stream	0.637	25.64			0.287*

Table 3.6. Independent estimates of population size for isolated cutthroat trout populations from genetic and from environmental data. N_e is based on an estimated loss in heterozygosity of $1/2N_e$ per generation. Census N is estimated by multiplying the amount of habitat by estimated fish density.

Site Code	Ne from He	Census N	Ne/N
DNA	10,068	20,710	0.49
DSA	5,051	5,443	0.93
JEA	3,931	977	4.03
MHA	1,497	648	2.31
NAA	7,637	20,150	0.38
RGA	1,469	2,706	0.54
WCA	221	1,110	0.20
WFA	1,647	9,867	0.17
HLA	3,991	14,000	0.29
LPA	2,966	1,400	2.12
MAA	1,885	6,388	0.30
POA	3,342	8,900	0.38

Figure 3.1. Typical bedrock waterfall that forms a complete and permanent barrier to upstream fish migration. For scale, note the person to the right of the base of the falls.

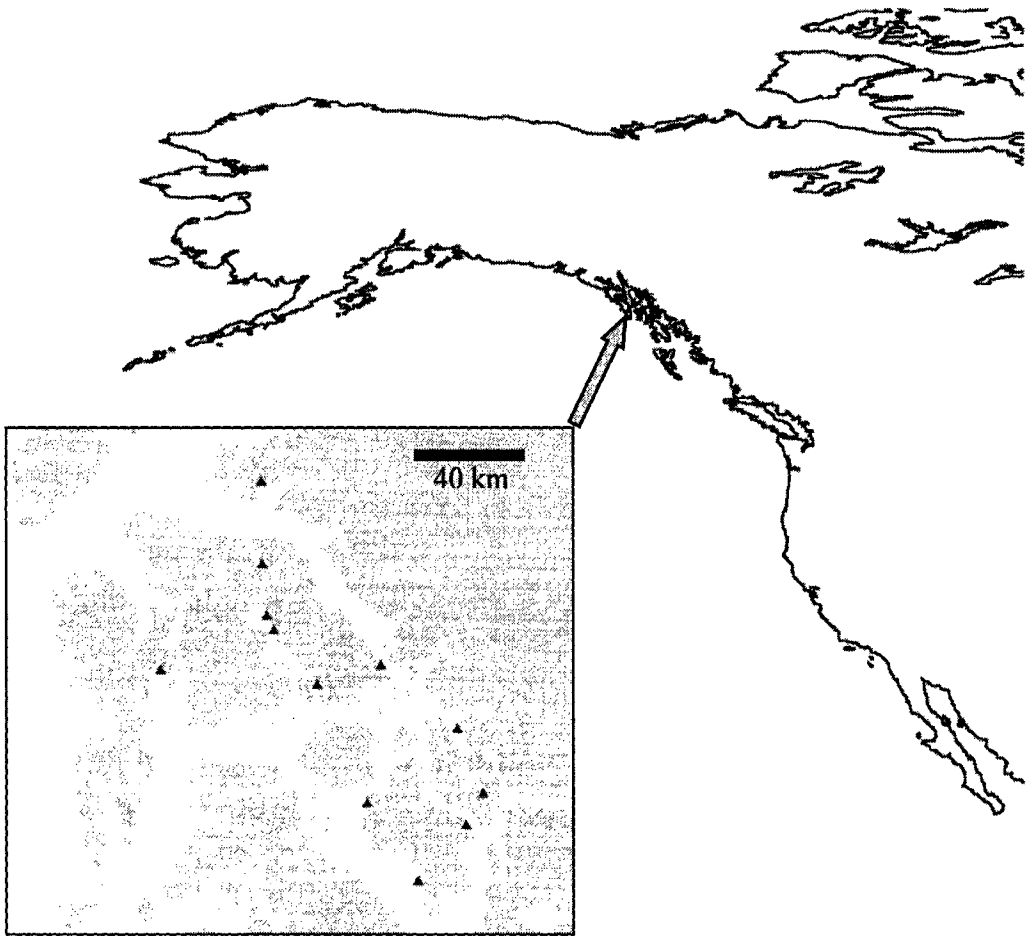

Figure 3.2. All study sites were located between 56°N and 57°N in the central portion of coastal southeastern Alaska.

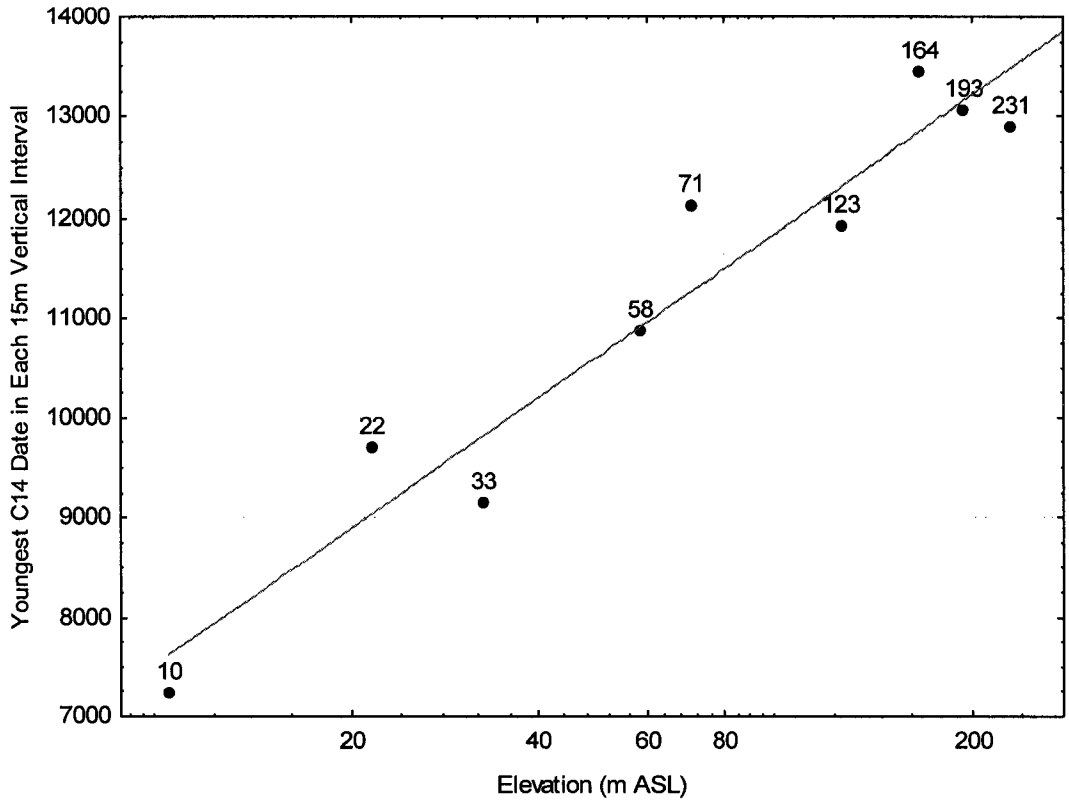

Figure 3.3. Isolation time in years related to log-transformed elevation (r^2=0.92; $p < 0.001$). Point labels are elevation in meters ASL. Isolation times are the ages of the youngest known uplifted marine sediments from each 15m vertical elevation stratum regionwide.

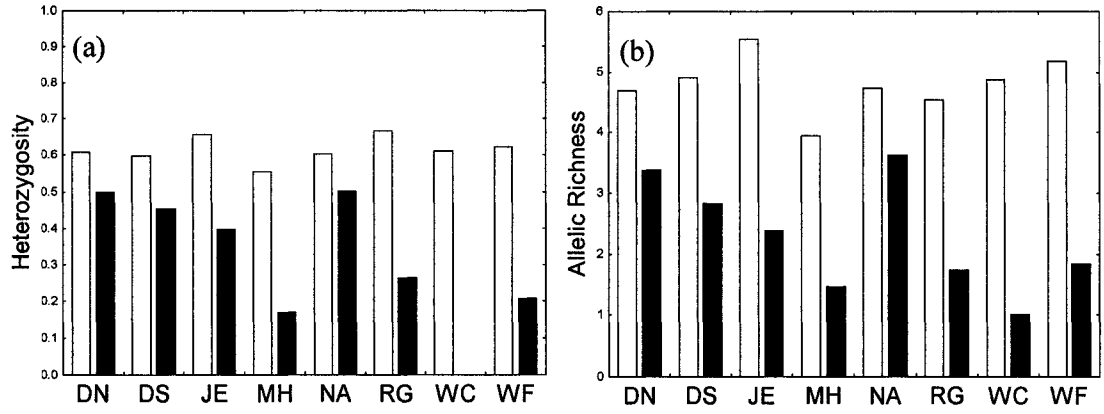

Figure 3.4. Within-population genetic variation for coastal cutthroat trout populations. Open bars are the below-barrier (non-isolated) populations and closed bars are the above-barrier (isolated) sample from the same stream. (a) Mean heterozygosity for each population. (b) Mean number of alleles per locus for each population.

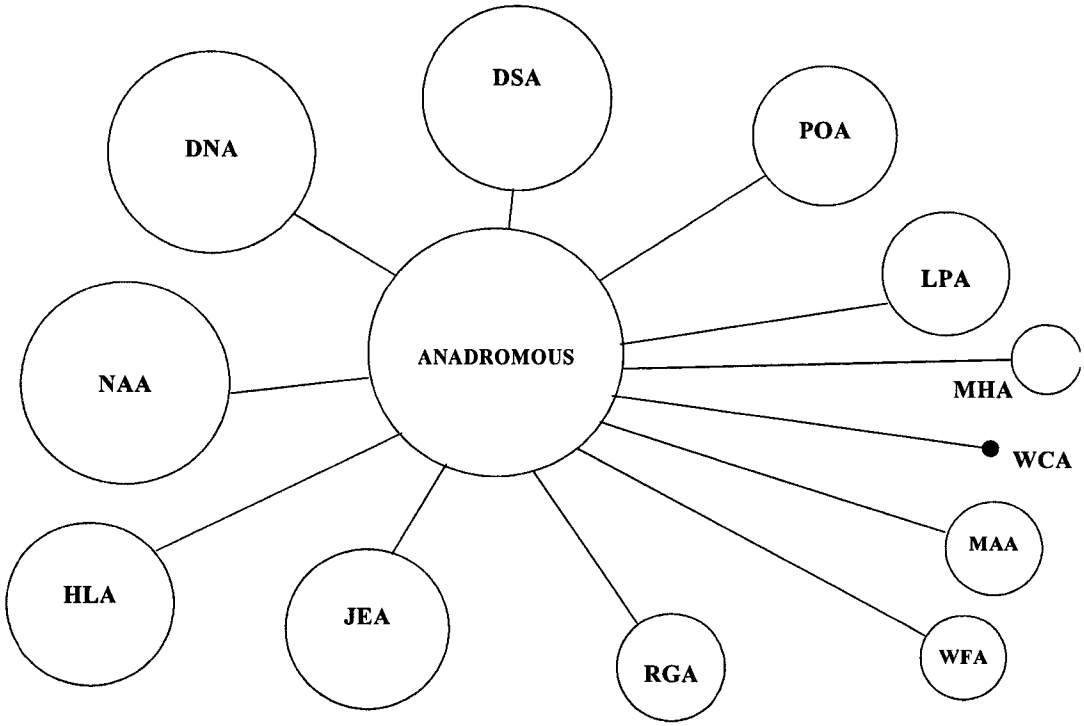

Figure 3.5. Relative differences in genetic variation between above- and below-barrier population pairs. ANADROMOUS represents the pooled below-barrier anadromous population. Diameter of each circle is proportional to expected heterozygosity in the corresponding above-barrier population. Length of each connecting line is proportional to F_{ST} between the above- and below-barrier population for that stream.

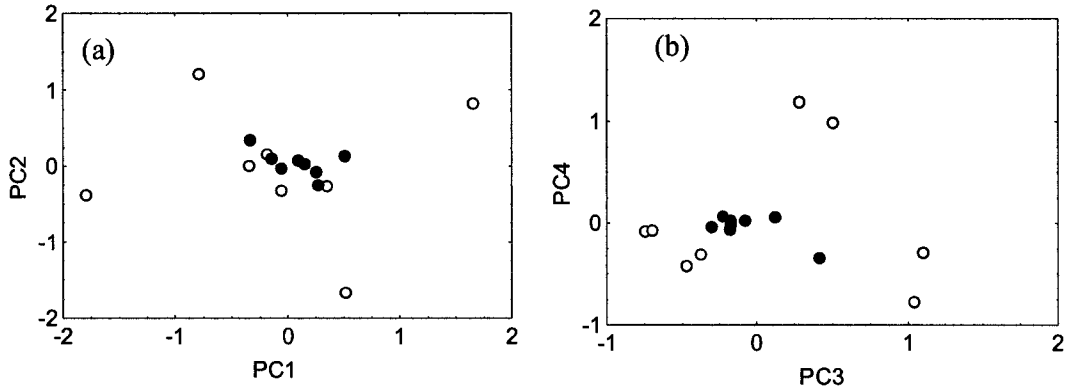

Figure 3.6. Principal components analysis of allele frequency variation between sites. Solid dots represent below-barrier populations and open dots are above-barrier populations. (a) PC1 (explains 25.4% of variation) vs. PC2 (explains 18.2%). (b) PC3 (explains 14.8%) vs. PC4 (explains 11.6%)

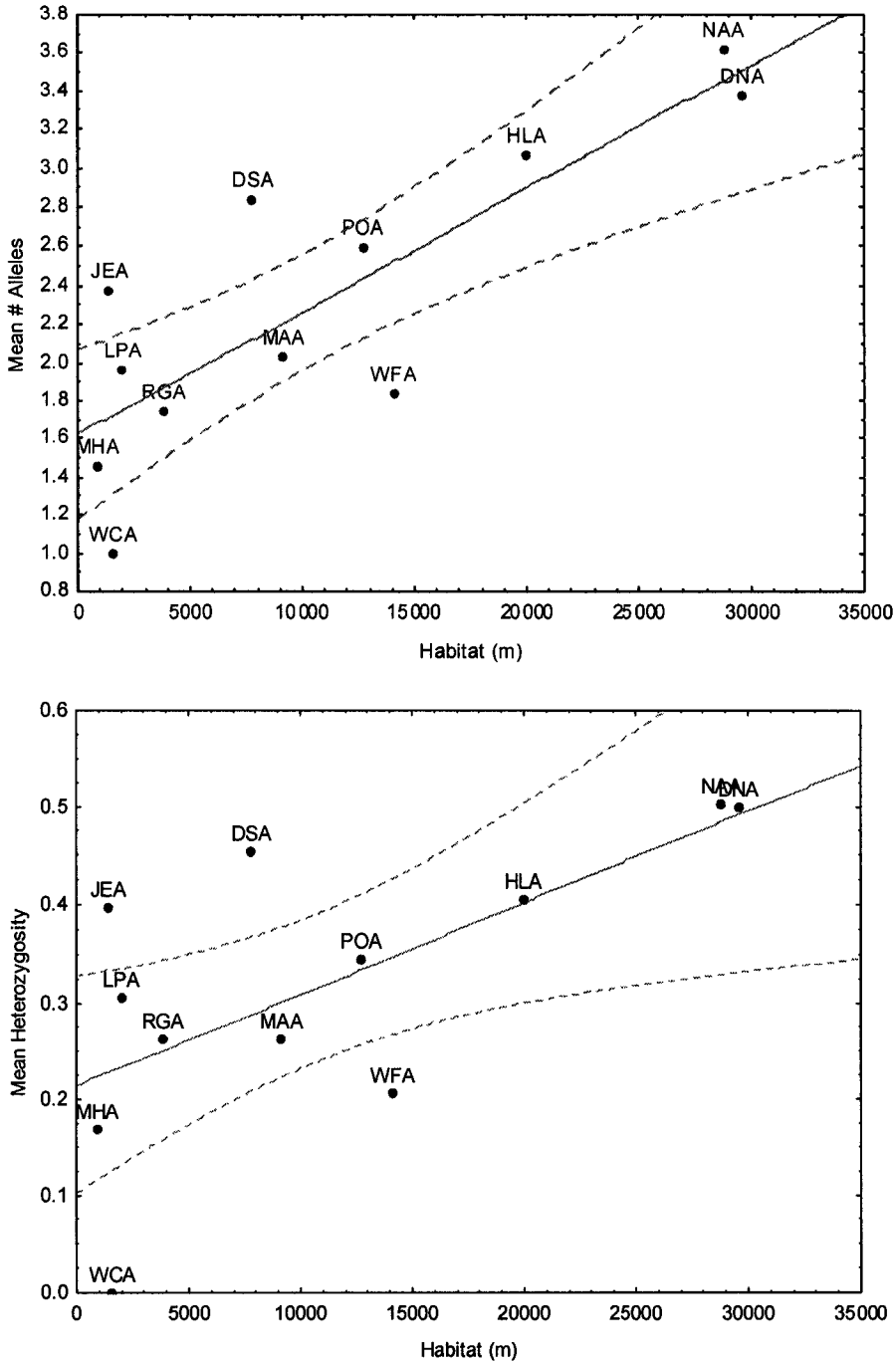

Figure 3.7. (a) Correlation between allelic richness and habitat length for 12 isolated populations. (r = 0.83). (b) Correlation between expected heterozygosity and habitat length (r = 0.65). Dotted lines represent 95% confidence interval.

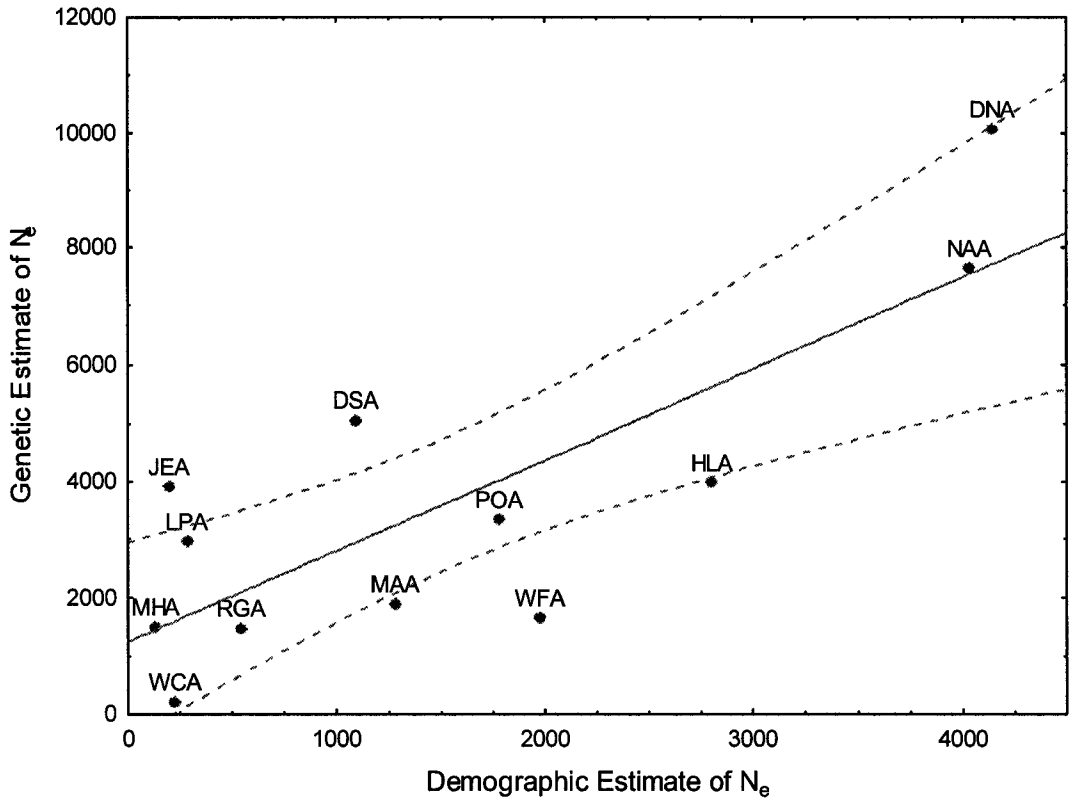

Figure 3.8. Correlation between two estimates of effective population size (N_e) for 12 isolated populations of coastal cutthroat trout (r = 0.80). Genetic estimate is calculated from loss in heterozygosity. Demographic estimate is calculated from habitat length and fish density, assuming $N_e/N = 0.2$. Dotted lines represent 95% confidence interval.

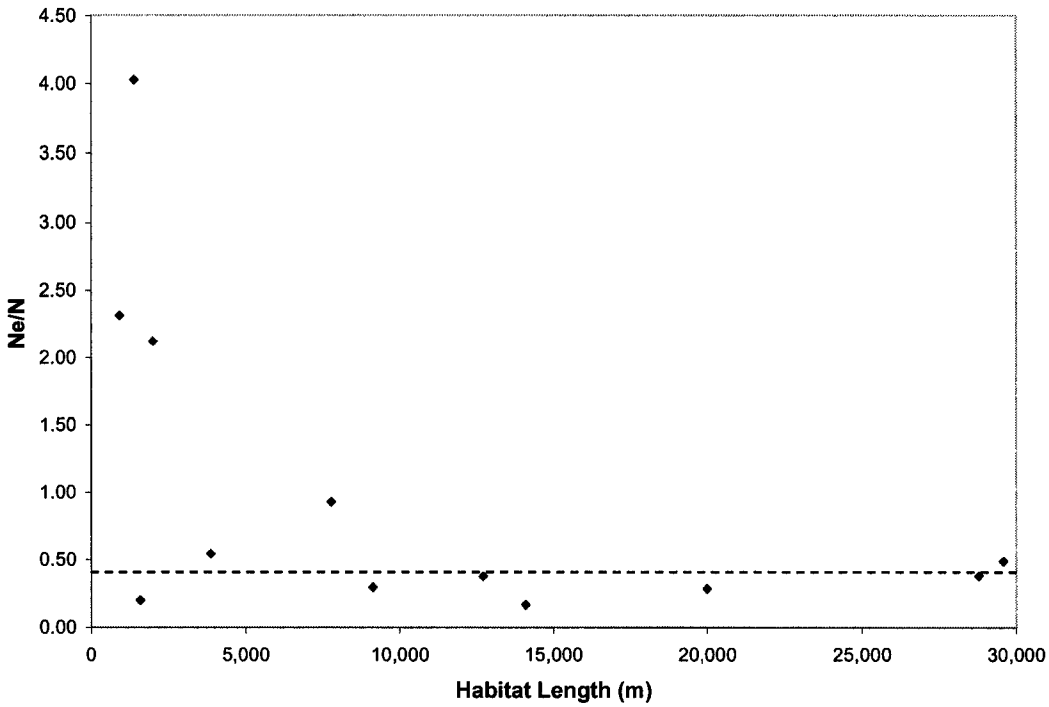

Figure 3.9. N_e/N ratio related to the length of habitat available to an isolated population. Dashed line indicates the median observed N_e/N ratio.

CHAPTER 4 – Long-Term Persistence of Small Isolated Fish Populations

ABSTRACT

We examined the conditions under which small, naturally isolated populations of stream-resident salmonids appeared to persist or fail in order to better understand the mechanisms that determine likelihood of persistence. We sampled pristine habitat above waterfalls in southeastern Alaska, where post-Pleistocene uplift has left many stream-resident populations of coastal cutthroat trout (*Oncorhynchus clarki clarki*) and Dolly Varden (*Salvelinus malma*) completely isolated from immigrants for thousands of generations. In 124 sites sampled, we found a 90% likelihood that populations of coastal cutthroat trout or Dolly Varden would be present when there was more than 5.5 km of linear habitat available, even with no lakes or ponds to buffer them from environmental extremes. Conversely, there was a less than 50% likelihood of finding either species present in streams with less than about 1.5 km of habitat. The upper threshold corresponds to an effective population size (N_e) of 440, which provides strong empirical support for the popular rule of thumb that recommends a minimum N_e of 500 to ensure long-term population persistence. The minimum habitat length required to support Dolly Varden populations appeared to be 65%-75% less than for coastal cutthroat trout; Dolly Varden was often the only species present in the smallest inhabited streams. Furthermore, Dolly Varden consistently achieved much higher densities when no other fish species was present than did coastal cutthroat trout. When both species were present, there was little difference, on average, in their densities, and the presence or absence of Dolly Varden seemed to have little effect on the density of coastal cutthroat trout.

Minimum adult census population sizes based on these density measurements were on the order of a few thousand individuals. The greater densities achieved when Dolly Varden were the only species present suggests that their population size is suppressed in the presence of cutthroat trout, presumably due to competition. Our results show that some small populations can persist in isolation in quite restricted habitat fragments, although over thousands of years they have measurably higher vulnerability to extinction than populations in larger fragments. For Dolly Varden in particular, that isolation from other species may play a role in enhancing persistence. We propose that species interactions may play a role in population persistence for other species of trout and char as well, and that disturbance-adapted salmonids may be able to persist in smaller amounts of isolated habitat than has been previously suggested. From a management standpoint, isolation within highly restricted geographic areas makes these populations of interest not only for their extinction risk, but also because they hold potential to be valuable indicators of the effects of localized anthropogenic development.

INTRODUCTION

While the extirpation of small populations is generally a stochastic process, Brown (1995) has argued that it is possible to identify factors that favor the probability of extirpation or extinction. In addition to stochastic events, there are deterministic factors that lower survival or growth rates in predictable ways. Rieman et al. (1993) have reviewed extinction processes as they relate to salmonid fishes. Destruction of spawning habitat, for instance, means that fewer fish will be able to find a place to spawn (assuming full utilization of the resource). The consequent reduction in population size

increases vulnerability to stochastic processes such as genetic drift and catastrophic environmental disturbance. While they are not predictable, stochastic events are not uncommon. Populations that are not threatened in other ways normally recover from all but the most catastrophic of stochastic events. However, populations that are small, either due to prior stochastic events or deterministic processes, are at increased risk of extinction from the next stochastic event. This is what Caughley (1994) termed the "small population paradigm".

How small is small? This question was addressed from a genetic perspective in Soule and Wilcox (1980), where the so-called 50/500 rule of thumb for short- and long-term population persistence first appeared. This rule of thumb states that an effective population size (N_e) of 50 is required to avoid inbreeding depression in the short term, while an N_e of 500 individuals is needed to retain evolutionary potential over the longer term (Franklin 1980). Subsequent debate has produced estimates of effective minimum viable population size of between 500 (Franklin & Frankham 1998) and 5000 (Lynch & Lande 1998), but again these theoretical numbers are derived only from the desire to retain some specified level of genetic variation. Other ecological factors, such as the spatial extent of the habitat a population occupies, its location relative to key disturbance events, the presence of possible refugia from disturbance, and conditions in its environment that may increase the frequency, magnitude, or spatial extent of disturbances, might be of equal or greater importance in determining the persistence of population isolates.

The effects of environmental and demographic stochasticity are more specific to a particular population in a particular setting, as they depend on population-specific vital

rates and site-specific environmental disturbance regimes. While environmental and demographic stochasticity can be modeled (Morris & Doak 2003; Shaffer 1981), it is rarely easy to obtain parameters for such models, making it difficult to know how realistic the models are (Beissinger 2002). If it is difficult to parameterize a model for a single population, it is that much more difficult to model extinction risk for a number of populations when setting priorities for conservation. What is sorely needed is a way to quickly identify which populations, of many, are closest to the edge. Is it necessary to understand all the factors that influence persistence and how they interact, or are there key indicators that will do the job?

Freshwater fish populations, as a group, are particularly threatened by anthropogenic development (Martin-Smith & Laird 1998; Warren & Pardew 1998). Development often centers on areas adjacent to water bodies, and runoff carries its products into fish habitat, where they are concentrated and degrade the quality of the habitat for fish. Alteration of riparian vegetation changes environmental characteristics in streams and rivers and reduces the supply of cover, food, and other key determinants of habitat value. Intentional fragmentation of fish habitat by dams, and unintentional fragmentation by poorly designed road crossings (Trombulak & Frissell 2000), is common. Because salmonids diverge relatively rapidly into subspecies and populations (Waples 1991), many distinct populations have been impacted and are potential candidates for conservation measures (Baker et al. 1996; Johnson et al. 1999; Schmidt 1997; Slaney et al. 1996; Stouder et al. 1997). There is a profound need for guidelines to identify which populations are at highest risk of extinction.

Population extinction is a stochastic process that takes an indeterminate but usually lengthy time to occur and thus to study, yet the need for guidelines for prioritizing salmonid conservation is immediate. To shortcut this constraint, we sought to examine natural extinction processes already underway. In southeastern Alaska, numerous small populations of resident salmonids have already been isolated for many generations by isostatic rebound. These populations were founded from saltwater early in the Holocene when the ice that covered the entire region during the Pleistocene first receded. As the land rebounded from the weight of the ice, geological discontinuities were often exposed as streams emerged from saltwater. These exposed bedrock waterfalls prevented further immigration to upstream populations, and created a widely replicated natural experiment in the long-term persistence of isolated fish populations (Hastings 2005, ch. 2).

We investigated the extent to which the likelihood of persistence of an isolated population could be predicted from easily measured ecological variables, particularly the amount of available habitat. For naturally isolated populations of stream-resident coastal cutthroat trout (*Oncorhyncus clarki clarki*) and Dolly Varden (*Salvelinus malma*) in southeastern Alaska, we asked these questions: (1) what are the most restricted settings in which isolated populations are known to have persisted; (2) how well is population persistence predicted by the amount of habitat available, for each species; (3) does a longer isolation period increase the amount of habitat required for the same likelihood of persistence; and (4) does the presence or absence of another salmonid species affect the likelihood of population persistence. Unlike much of the remainder of North America, headwater streams in southeastern Alaska have been little subject to fish stocking, presenting a uniquely unencumbered opportunity to draw inference from a regional-scale

study of natural population occurrences. While the study area is not entirely pristine, the relatively limited history of natural resource development and environmental alteration by dams further reduces the complexity of interpreting patterns in population occurrence when compared with studies of more anthropogenically altered ecosystems.

METHODS

We identified settings in which natural fish populations had been established and subsequently isolated in small subdrainages for many generations. In southeastern Alaska, such settings are relatively numerous, where small amounts of suitable fish habitat are found upstream of permanent and complete migration barriers (bedrock waterfalls). The habitat above these waterfalls was accessible from saltwater after the retreat of ice in the late Pleistocene, but fish populations there became isolated from potential immigrants when post-Pleistocene isostatic rebound exposed geological discontinuities in the stream channel (Hastings 2005, ch. 2). Where fish were absent from suitable habitat above a permanent upstream movement barrier, we assumed that an isolated population there had failed to persist. For settings with and without present-day fish populations, we then collected data about the conditions that appeared to support or limit longterm population persistence.

Study Design

We visited sites upstream of bedrock waterfalls throughout the study area to evaluate fish species presence and watershed characteristics (Figure 4.1). Each sample site consisted of the entirety of the contiguous habitat available to an isolated population

of fish living upstream of a permanent and complete movement barrier. We defined "suitable habitat" for resident salmonids to be any stream channel less than 25% gradient that would have been continuously connected to saltwater at the end of the Pleistocene, prior to the start of Holocene uplift. Lakes and ponds provide a refuge from stressful environmental conditions and, at least at low elevations in southeastern Alaska, are almost universally associated with persistent fish populations regardless of the amount of attached stream habitat. In order to focus on the most limiting conditions for population persistence, streams with connected lakes were excluded from this study.

We sampled widely at both high and low elevations and in small and large drainages. The high cost of logistics required us to be somewhat opportunistic in selecting study sites. In addition, we followed an adaptive sampling process, deliberately filling holes along the spectrum of drainage sizes as the study progressed. We especially concentrated on identifying and examining streams where isolated populations had apparently been extinguished by natural causes (*i.e.* apparently suitable but presently unoccupied habitat above a waterfall), since this was simultaneously the stratum of greatest interest and of most limited occurrence. As with other studies that use incidence functions to draw conclusions about population persistence (Dunham & Rieman 1999), our analytic approach was less dependent on the even spatial distribution of sample sites than on the distribution of adequate numbers of samples along the gradients of factors expected to exert a strong influence on persistence.

Potential sample sites were initially identified using two regional spatial databases (GIS) that described stream reach morphology and the locations of movement barriers, respectively. The stream reach database was previously developed for the Tongass

National Forest by interpreting stereo pairs of aerial photographs (USDA Forest Service 1992). Channel segments of 100 m or longer were assigned to a geomorphological channel type according to a classification scheme that allowed potential fish habitat to be easily distinguished from reaches too steep to support any fish populations. All streams visible on aerial photographs were mapped; in practice this meant that channels as narrow as 1 m were mapped, but the upper extents of many streams were obscured by vegetation and not detected unless they were sufficiently incised to be apparent from the surrounding landform. Thus the database contains most, but not all, fish habitat in southeastern Alaska.

For the second spatial database, we compiled information about nearly 1000 potential upstream movement barriers from a variety of sources. We reviewed all stream surveys published for southeastern Alaska (dating back to 1959) by state and federal biologists seeking to identify the upstream limit of anadromous fish presence, generally some form of upstream movement barrier. In addition, many barriers were identified by visual interpretation of stereo aerial photographs as part of the process of validating the Tongass National Forest stream channel type classification (USDA Forest Service 1992). Finally, we interviewed biologists and hydrologists from each Ranger District of the Tongass National Forest, several offices of the Alaska Department of Fish and Game, and both of the Regional Aquaculture Associations that serve southeastern Alaska.

Using these two spatial databases, we generated an initial list of almost 600 locations in the central third of southeastern Alaska where there appeared to be fish habitat above a potential barrier. We screened out locations where the elevation at the top of the barrier was believed to be too high to have permitted post-Pleistocene

colonization (Hastings 2005, ch. 2). We avoided sites with more than one barrier below the maximum colonizable elevation, because of the expectation that the dynamics of persistence would be more complex for subdivided populations than for single populations. To avoid the confounding effects of anthropogenic developments on population persistence, we generally focused on watersheds with no history of industrial-scale human disturbance (*e.g.* timber harvest, mining, or roads).

In our definition of barriers, we did not include beaver dams, tidal barriers, velocity barriers, manmade barriers, or generally anything other than a natural bedrock streambed at a high enough gradient to block upstream passage by adult steelhead (*Oncorhynchus mykiss*), the life stage and species among the anadromous fish species found in the region that has the greatest capacity to surmount upstream movement barriers (USDA Forest Service 2001a). USDA Forest Service (2001a) defines what would be required to stop passage of an adult steelhead. Three criteria are given: (1) a vertical falls of more than 13' in height, where vertical is defined as at least a 70° slope; (2) a steep channel (not vertical) where a 24% gradient is sustained for at least 25', or a 12% gradient for at least 225', without resting places en route; or (3) a vertical falls more than 4' but less than 13' that lacks a plunge pool at the base whose depth is at least 1.25 times the height a fish must jump to surmount the barrier. In most cases, barriers on the streams we sampled fit the first criterion (Figure 4.2).

Upstream movement barriers are not necessarily downstream movement barriers, and we are unaware of any criteria for what would constitute a downstream movement barrier. Undoubtedly some fish from the populations we sampled do successfully descend waterfalls, but in this study we were not concerned with the fate of emigrants,

only that the populations isolated above barriers had no contact with immigrants. As reported elsewhere (Hastings 2005, chapter 3), we used genetic evidence to confirm that populations above upstream movement barriers fitting the criteria above showed no evidence of interbreeding with immigrants from downstream populations over many generations.

We estimated the time each above-barrier population became isolated from radiocarbon dates for shell fragments found within or above uplifted glaciomarine sediments at various elevations throughout southeastern Alaska (Hastings 2005, ch. 2). The time of deposition of the sediments establishes the maximum amount of time that could have elapsed since a site at that elevation emerged from the sea.

Data Collection

We visited sample sites with three goals in mind: (1) to verify the presence of a complete barrier with a habitable stream reach above; (2) to establish which fish species, if any, were present above the barrier; and (3) to collect information about the amount and quality of the habitat above the barrier. Barrier verification was done by taking physical measurements according to the barrier criteria described above (USDA Forest Service 2001a). Fish presence was initially assessed by DC backpack electroshocking. If no fish were detected by electroshocking, we further tested for fish presence using at least 25 minnow traps, baited with salmon eggs. Traps were set throughout the entire length of above-barrier habitat and left to soak overnight. We surveyed the entire length of fish habitat above the barrier on foot when the length did not exceed 1.5 km. In larger drainages, fish habitat length was estimated using the GIS database of stream reaches.

We estimated the density of cutthroat trout and Dolly Varden in 24 streams annually for up to six years. Density was estimated by three-pass removal sampling using minnow traps baited with salmon eggs (Bryant 2002). Many of these estimates were conducted by the U.S. Forest Service as part of its annual monitoring program to detect impacts of timber harvest and road building on resident fish in the Tongass National Forest (USDA Forest Service 2000, 2001b, 2002c, 2003). These were point density estimates for representative, above-barrier stream reaches between 70m and 170m long.

Additional Presence-Absence Data

We augmented our fish presence dataset by incorporating sites used for resident fish population monitoring as part of the Tongass National Forest annual monitoring program (USDA Forest Service 2000, 2001b, 2002c, 2003). While we were rarely comfortable accepting an assessment of fish *absence* that we did not verify, we did incorporate records of fish *presence* above barriers in roaded watersheds from the so-called "road condition surveys" (RCS) conducted by the Tongass National Forest. At each location where a road crosses a stream with fish-bearing potential, RCS teams collect data about fish presence and stream channel characteristics to evaluate the adequacy of fish passage at road-stream crossings. From a database of over 3200 locations where roads crossed fish habitat, we identified over 500 sites where a barrier was believed to exist downstream of the road crossing. We also added to our verified fish presence dataset 16 streams that are being used by the Tongass National Forest to monitor annual trends in population and habitat for resident fish above barriers. Both the

barrier and species presence information for these streams was field-verified following a protocol equivalent to our own.

Data Analysis

All statistical tests were conducted using Statistica V 6.0 (Statsoft Inc.). We used logistic regression to predict the probability of persistence as a function of available habitat and isolation period. Habitat amount was log-transformed to correct for non-normal distribution of sample sites along the habitat amount gradient. We chose base-2 logarithms to simplify the interpretation of results (an increase of 1 in the log-transformed value represents a doubling of the untransformed habitat amount).

RESULTS

Presence/Absence of Fish Populations

We assessed fish species presence above permanent waterfalls in 124 streams (Figure 4.1). We field-verified presence/absence and barrier characteristics for 66 (53%) of these streams. Data for the remaining 58 streams came from field surveys conducted by the Tongass National Forest (TNF) and were screened but not field-verified by us. We accepted most TNF assessments of fish presence, but few TNF assessments of fish absence unless we were able to verify them ourselves. That meant that the ratio of streams with fish absent to streams with fish present was much higher in the verified dataset (20:46) than in the unverified dataset (9:49). However, for streams where isolated fish populations were detected, the relative percentages of streams with only Dolly Varden, only coastal cutthroat trout, or both species present did not differ between the

two datasets (Figure 4.3). Because the two species are generally easily detected and distinguished, and because no species bias was detectable in the unverified dataset, we merged the two datasets (verified and unverified) for our analyses.

The length of above-barrier habitat at our sites varied from 200 m to 50,100 m (Figure 4.4). No fish were found in 29 (23%) of the 124 streams we sampled. (Because the proportion of fishless streams we report was strongly biased upward by our sampling scheme, this number should not be taken to represent the actual percentage of fishless, isolated streams.) Both coastal cutthroat trout and Dolly Varden were present in 33 (27%) of the streams, only coastal cutthroat trout in 21 (17%) of the streams, and only Dolly Varden in 41 (33%) of the streams. We found isolated Dolly Varden in streams as short as 415 m long. Isolated coastal cutthroat trout populations were found in streams as short as 700 m. The longest fishless stream we found had 2300 m of habitat above the barrier. One or both species were generally present in streams with 2 km or more of habitat, and generally absent from streams with less than about 1.5 km of habitat. The threshold zone of 1.5-2 km for fish presence-absence did not differ substantially among streams where only coastal cutthroat trout, only Dolly Varden, or both species were present, except that the smallest streams had only Dolly Varden present and the largest streams nearly always had both species present.

There was a greater than 50% likelihood of finding at least one species present in streams longer than about 1 km, and a 90% likelihood of finding fish present in streams over 4.4 km long (Table 4.1, Figure 4.5). Slightly less habitat was required for a given likelihood of finding Dolly Varden than for coastal cutthroat trout. More habitat was required to support both species in sympatry than to support either species alone (Table

4.2). When comparing streams with only Dolly Varden and streams with both Dolly Varden and coastal cutthroat trout, almost 10 km of habitat was required for a better than 50% likelihood of finding the two species together. Coastal cutthroat trout were less likely to be found alone; only 2 km of habitat were required for a better than 50% likelihood of finding Dolly Varden in the same stream.

Isolation Period

Estimated isolation periods ranged from 5,400 to 13,100 years (median 11,000 years). Adding isolation period to the overall logistic regression model did not add significantly to the power to predict population persistence for either species. However, when we considered only the smallest populations, there was a positive correlation between the length of the isolation period and the amount of habitat required to sustain a fish population (Figure 4.6). Our definition of "smallest populations" included all populations from streams no longer than the longest verified fishless stream (2,300 m), which coincided with the lower quartile of all streams where fish were found above barriers. This set comprised 22 streams, 10 of which contained coastal cutthroat trout and 17 of which contained Dolly Varden. The correlation between length of isolation period and habitat required for persistence of at least one species was significant ($r = 0.52$, $p = 0.01$). Looking at the species individually, the correlation was weaker but still detectable (for coastal cutthroat trout, $r = 0.58$ and $p = 0.06$; for Dolly Varden, $r = 0.47$ and $p = 0.06$). These relationships were not simply due to shorter streams being found at higher elevations, as the correlation between habitat length and elevation was not significant for the set of *all* sampled streams less than 2400 m long ($r = .19$, $p = .19$).

Species Composition

Coastal cutthroat trout were present in 54 (44%) of streams, while Dolly Varden were present in 74 (60%) of streams. Where coastal cutthroat trout were found, 39% of the time they were the only species present. In contrast, Dolly Varden were not only more common, they were also more likely to be the only species present where they were found (55% of streams containing Dolly Varden). With one exception, these two species were the only ones we found above waterfalls in streams (not connected to lakes) in southeastern Alaska. The exception was a single isolated population of western brook lamprey (*Lampetra richardsoni*) sympatric with both coastal cutthroat trout and Dolly Varden in a relatively large mainland drainage.

Fish Density

Adult cutthroat trout density ranged from 0.01 to 1.29 fish/m (mean: 0.47 +/- 0.08) over 53 sampling occasions in 11 streams where Dolly Varden were also present, and from 0.19 to 0.82 fish/m (mean: 0.39 +/- 0.08) over 23 sampling occasions in the four streams from which Dolly Varden were absent (Figure 4.7). The density of adult Dolly Varden ranged from 0.02 to 1.10 fish/m (mean: 0.34 +/- 0.07) over 50 sampling occasions in the 11 streams where cutthroat trout were also present, and was lower than the density of cutthroat trout in 10 of those streams. However, in nine streams where cutthroat trout were absent, Dolly Varden densities were much higher, ranging from 0.34 to 5.42 fish/m over 29 sampling occasions, with a mean of 1.84 +/- 0.51 fish/m. We express fish density as fish/m rather than fish/m^2. However, we found high correlation ($r = 0.89$ for

Dolly Varden and r = 0.90 for coastal cutthroat trout, p = 0.00 for both) between the two measures in 24 small streams where both length and area of sampled habitat were known. Adult, stream-resident coastal cutthroat trout and Dolly Varden in southeastern Alaska are typically about 80 – 120 mm fork length in size (Figure 4.8) and do not exceed about 205 mm.

DISCUSSION

How Small is Small?

We found populations of both coastal cutthroat trout and Dolly Varden persisting in less than a kilometer of stream, despite having been isolated for thousands of generations. Our density measurements suggest that the smallest populations we identified number about 600 adult fish (Table 4.3). This minimum observed population size was approximately the same regardless of species and of whether just one or both species were present, suggesting that stream carrying capacity for these resident salmonids could be relatively species-independent. Looking more broadly at our presence-absence data, we estimated that populations would consist of 1000-3000 adult fish in streams where the amount of habitat is equal to the length threshold corresponding to a 50% likelihood of long-term persistence. The variation in range is due to our observation that Dolly Varden populations in the absence of other fish species are denser, and thus larger, than coastal cutthroat trout populations or Dolly Varden populations sympatric with coastal cutthroat trout.

How Well Does Habitat Amount Predict Population Persistence?

We found a very strong correlation between amount of habitat available and the likelihood of population persistence, as have others (Dunham & Rieman 1999; Koizumi & Maekawa 2004; Morita & Yamamoto 2002). However, we also found a distinct threshold zone between 1.5 km and 2.0 km of stream length. It appears that population persistence is nearly assured for stream-resident cutthroat trout and Dolly Varden in southeastern Alaska when a population has access to at least 2.0 km of stream, yet is highly unlikely in less than 1.5 km of habitat. Habitat quantity is likely to be correlated with a number of factors that influence population persistence. Assuming that population size is constrained by available habitat, they include the demographic and genetic stochasticity that are the consequences of small population size (Frankham 1996; Gilpin & Soule 1986). In addition, very small amounts of habitat may not include some of the habitat heterogeneity found in the larger landscape. If a type of habitat required for a particular life history stage is missing or in short supply – deep pools, for instance – the carrying capacity of a given amount of habitat may be reduced (Dunning et al. 1992). Larger drainages are more likely to include off-channel ponds, a critical overwintering habitat for juvenile salmonids (Swales & Levings 1989, M.D.Bryant *pers. comm.*).

Others have suggested that somewhat larger amounts of habitat are needed to sustain isolated populations of stream-resident salmonids than the 5.5 km we observed for a 90% likelihood of persistence. Hilderbrand and Kershner (2000) concluded that 8-25 km of stream were necessary to support a minimum viable census population size of 2,500 inland cutthroat trout in small streams, assuming fish densities similar to what we observed. Harig and Fausch (2002) looked at the short term persistence (1-31 years) of

translocated populations of inland cutthroat trout (*O. c. stomias* and *O. c. virginalis*) and found that a watershed area of more than 14.7 km^2 was required to predict a greater than 50% probability of finding a thriving population of cutthroat trout at 3-31 years (median 13 yrs.) after translocation. Leopold et al. (1964) provide a general allometric relationship between channel length and drainage area:

$$L = 1.4\,A^{0.6} \quad (1)$$

where L is length in miles and A is area in square miles. Using this formula to predict channel length from drainage area, the threshold suggested by Harig and Fausch (2002) would correspond to about 6.4 km of stream. That requirement is again greater than the amount of habitat that we found was needed for persistence over a much longer period. Short-term persistence of stream-resident salmonids was studied empirically by Morita and Yamamoto (2002), who examined populations of white-spotted char (*S. leucomaenis*) isolated above dams built in the previous 50 years. They concluded that the minimum watershed size needed to maintain a population over this period was 2.3 km^2, equivalent to about 2.1 km of linear stream channel.

Our study was the first in which the long-term persistence of stream-resident, headwater salmonid populations was inferred from empirical data unencumbered by complications due to extensive human alterations of the landscape. Such alterations not only affect the quantity, quality, and connectivity of habitat patches in complex ways, but they may also result in competitive displacement or genetic disruption of populations by the introduction of non-native or hatchery fish. Furthermore, the populations we studied

are highly unusual among salmonids, even in southeastern Alaska, in being free of human harvest pressure. The smaller amount of habitat that appears to be required to sustain fish populations in southeastern Alaska when compared to the contiguous United States could easily be a result of the absence of these kinds of anthropogenic disturbance. There are other possibilities. Regardless of human influence, the headwater stream environment in southeastern Alaska may be more stable, or at least less less stressful to fishes. Disturbance regimes in southeastern Alaska are primarily storm-driven and relatively small scale. It is rare, for instance, for an entire landscape to be returned to a state of primary succession, as sometimes occurs with catastrophic wildfires in the western United States. Stochastic environmental events such as a heat wave or drought can force populations through bottlenecks, and these may be less common, or less extreme, in southeastern Alaska. Importantly, it is when multiple stochastic events occur sequentially or concurrently that population persistence is most threatened. The greater number of potential stressors for headwater fish populations in the contiguous United States could help to explain why these populations might be more vulnerable than the ones we studied. We strongly caution against extending the specific results of our study to other regions without first accounting for these differences.

Isolation Period

We would expect the likelihood of population persistence to decrease over time, all other factors being equal, because of the stochastic nature of extinction processes. In this study, we did find evidence of this relationship. Populations at higher elevations would have been isolated longer, and we found fewer small populations as barrier

elevation increased. An alternate hypothesis for why more habitat might be needed at higher elevations would be that larger and deeper streams would be required to provide a refuge from the more stressful winter conditions away from sea level. However, the elevations involved (generally less than about 150 m ASL) are quite low when compared with the set of all resident fish stream reaches in the study area (Figure 4.9), suggesting that environmental conditions are not likely to be especially limiting at these lower elevations.

We express isolation period in terms of years, which might be relevant for environmental extinction processes but are not the appropriate units for demographic and genetic extinction processes, which act on generations. Unfortunately, the demography of isolated resident populations of coastal cutthroat trout and Dolly Varden has not been studied at all in southeastern Alaska, and has received little attention elsewhere that these species occur. We estimated a generation time of 3 years for stream-resident coastal cutthroat trout (Hastings 2005, chapter 3), but there is considerable uncertainty about this number and our estimate may have been low. Other studies have found that coastal cutthroat trout in similar settings rarely live longer than 4 years (June 1981; Wyatt 1959). However, we have a small amount of anecdotal evidence that stream-resident coastal cutthroat trout in southeastern Alaska may live for six years or more and Dolly Varden for at least 10 years (K. Munk and K. Hastings, unpublished data). Because the majority of glacial isostatic rebound occurs soon after the weight of the icesheet is removed, uplift in most of southeastern Alaska was largely complete by about 8,000 years ago. We estimated that most of the populations we studied have been isolated for 8,000 to 12,000 years. That would translate to somewhere between 800 and 6,000 generations, based on

the limited information we have about generation time for the stream-resident form of these two species. While this is a very imprecise estimate, these populations have clearly been isolated far longer than any populations fragmented by recent anthropogenic events. Thus the thresholds we identified for population persistence can be considered quite conservative over the shorter time spans on which natural resource development and conservation take place.

Species Interactions and Density

We found evidence that Dolly Varden density was suppressed in the presence of coastal cutthroat trout. Habitat segregation between salmonids has been widely documented (Dolloff & Reeves 1990; Glova 1987; Hearn 1987), with the general pattern that *Oncorhynchus* tends to outcompete sympatric *Salvelinus* when both are native. Northcote (1995) summarized numerous experiments conducted to identify competitive exclusion between cutthroat trout and Dolly Varden. These experiments were motivated by the observation that these two species tend to segregate spatially in both lakes (where cutthroat trout are found near the surface and closer to shore) and streams (where cutthroat trout occupy the center of the channel). Northcote's (1995) experiments were inconclusive, but the pattern of segregation, wherein cutthroat trout appear to consistently occupy the preferred habitat, was not.

Our estimates of cutthroat trout density are similar to estimates made for other species of cutthroat trout in inland headwater streams. Hilderbrand and Kershner (2000) report estimates of 0.20-0.35 fish/m for 3 subspecies of cutthroat trout across 38 streams. Like Hilderbrand and Kershner (2000), we chose to express fish density linearly, *i.e.*

fish/m rather than fish m^2. When fish density can be expressed in terms of stream length rather than area, it is a more generally useful number. Stream length can be easily derived from maps or aerial photographs, whereas determination of stream area generally requires a field survey.

Empirical Support for the 50-500 Rule

The 50-500 rule of thumb for recommended minimum population size (Soule & Wilcox 1980) has a strong theoretical foundation and has been widely applied, but empirical support for the rule has been hard to come by because of the long-term nature of the predictions. Our results show a surprisingly accurate alignment with the predictions of the long-term ("500") portion of the rule. An effective population size (N_e) of 500 would correspond to a census population size of about 2500 adult salmonids, based on an expected N_e/N ratio of 0.2 for this taxonomic group (Allendorf & Waples 1996). A population of 2500 adult fish at a typical density of 0.4 fish/m would require approximately 6.25 km of stream habitat. Our data indicate that about 5.5 km of habitat are required for a 90% likelihood of persistence, a very close fit with the 6.25 km predicted by the 50-500 rule. While one should always use caution when extrapolating beyond the conditions examined in an individual study, these results should bolster the confidence of those employing the 50-500 rule in situations where empirical support for its predictions is unavailable.

Management Recommendations

The landscape of southeastern Alaska has a high degree of natural fragmentation due to steep topography and the network of interspersed saltwater channels. However, stream networks here and elsewhere have been further fragmented in many areas by road-stream crossings not designed to pass resident fish (Kahler & Quinn 1998; Shea Flanders & Cariello 2000; Warren & Pardew 1998). One of the most immediate applications of our results will be to determine which resident fish populations are most in need of reconnection through restoration of fish passage at these crossings. For resident fish populations above a natural barrier that have been further fragmented by inadequate road-stream crossing structures (mainly high gradient or perched culverts), it is important to consider the amount of habitat both above and below each crossing. If either is less than about 1 km, restoring fish passage at that crossing should be a high priority if the habitat on both sides is to continue to support fish. A further consideration is that the uppermost habitable reaches of a natural stream represent a unique habitat type, shallower water with many small refuges from high flows due to step-pool morphology. This habitat type may be important to rearing juveniles if it allows them to escape predation and cannibalism from larger fish restricted to deeper stream reaches. Several studies are currently underway to examine seasonal use of high gradient headwater reaches by juvenile salmonids in southeastern Alaska (Bryant et al. 2004).

We found strong evidence that Dolly Varden densities are suppressed in the presence of coastal cutthroat trout. Similarly, Glova (1987) demonstrated suppression of coastal cutthroat trout densities in the presence of coho salmon (*Oncorhynchus kisutch*) and sculpins (*Cottus* spp.), an effect that we also observed (K. Hastings, unpublished

data). In southeastern Alaska, a number of fish passes have been built to allow anadromous salmon, principally coho, access to habitat previously occupied only by stream-resident Dolly Varden and coastal cutthroat trout. We caution that this action likely has unintended consequences for those previously isolated populations.

Isolation in headwater reaches has been proposed as a conservation strategy for inland cutthroat trout, where headwater populations are often the only remaining pure stocks (Kruse et al. 2001; Novinger & Rahel 2003). In evaluating this strategy, the focus has been on protecting headwater stocks from pathogens and from non-native species that compete and hybridize with the native stocks. However, it may also be important to consider competition from other native species present in headwater streams when assessing the viability of remnant populations. In particular, bolstering a native trout population with the addition of hatchery fish may result in unintended suppression of sympatric native char.

Small isolated fish populations offer an unparalleled opportunity to study population persistence in both natural and human-influenced settings. Much remains to be learned beyond what we have documented. Knowing the demographic characteristics of small, isolated populations would go a long ways towards an understanding of the mechanism for the dependence on habitat quantity that we saw. Stage-specific vital rates and population age distributions would allow the comparison of actual population persistence with that predicted by structured population viability analysis (Beissinger & McCullough 2002; Morris & Doak 2003). Knowledge of the annual variation in population size would help to establish the carrying capacity of a given amount of habitat. Any of these variables might prove a sensitive enough index to be used for

monitoring population changes in response to anthropogenic development, could an efficient means of measurement be devised. Monitoring the changing characteristics of completely isolated populations restricted to a small geographic area offer conservation biologists the best opportunity we have for understanding the effects of human activities on non-human organisms.

ACKNOWLEDGEMENTS

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Table 4.1. Amount of habitat required for long-term persistence of isolated stream-resident populations of coastal cutthroat trout (CCT) and Dolly Varden (DV). The set of streams where each species was found was compared with the 29 streams where no fish were found using logistic regression; all regressions were highly significant. The odds ratio shown is for a unit change in log2 (habitat length); each doubling in habitat length increased the likelihood of species persistence by the ratio shown. The 50% and 90% length thresholds are the lengths at which the likelihoods of species persistence were greater than 50% and 90%, respectively.

Species	*n*	*χ2*	*P*	*Odds Ratio*	*50% Length Threshold (km)*	*90% Length Threshold (km)*
Either	95	46.74	0.00	2.95	1.07	4.41
DV	74	42.96	0.00	2.80	1.26	5.54
CCT	54	45.22	0.00	3.67	1.73	5.58

Table 4.2. Amount of habitat required to support Dolly Varden (DV) and coastal cutthroat trout (CCT) in sympatry compared to streams where each species was found alone. The odds ratio is the increased likelihood of finding the other species present with each doubling of habitat length. The 50% length threshold is the length at which the likelihood of finding the other species present exceeds 50%. Thresholds for 90% likelihood of finding the two species in sympatry are not shown because they exceeded the length of the longest stream in our dataset by more than an order of magnitude.

Species	*n*	*χ2*	*P*	*Odds Ratio*	*50% Length Threshold (km)*
DV	41	4.01	0.05	1.38	9.45
CCT	21	2.58	0.11	1.36	2.14

Table 4.3. Estimated sizes of smallest isolated populations found ("minimum observed habitat length"), and expected sizes of populations in streams where the amount of habitat is equal to the length threshold corresponding to a 50% likelihood of long-term persistence ("50% threshold length"). Census estimates are based on length of available habitat and average density of adult fish of each species when no other species is present and when both species are present.

Species Present	*Minimum Observed Habitat Length (m)*	*Estimated Census N*	*50% Threshold Length (m)*	*Estimated Census N*
Alone				
Cutthroat trout	1585	618	2550	995
Dolly Varden	415	764	1660	3054
Together				
Cutthroat trout	700	329	2500	1175
Dolly Varden	700	238	2500	850
Total		567		2025

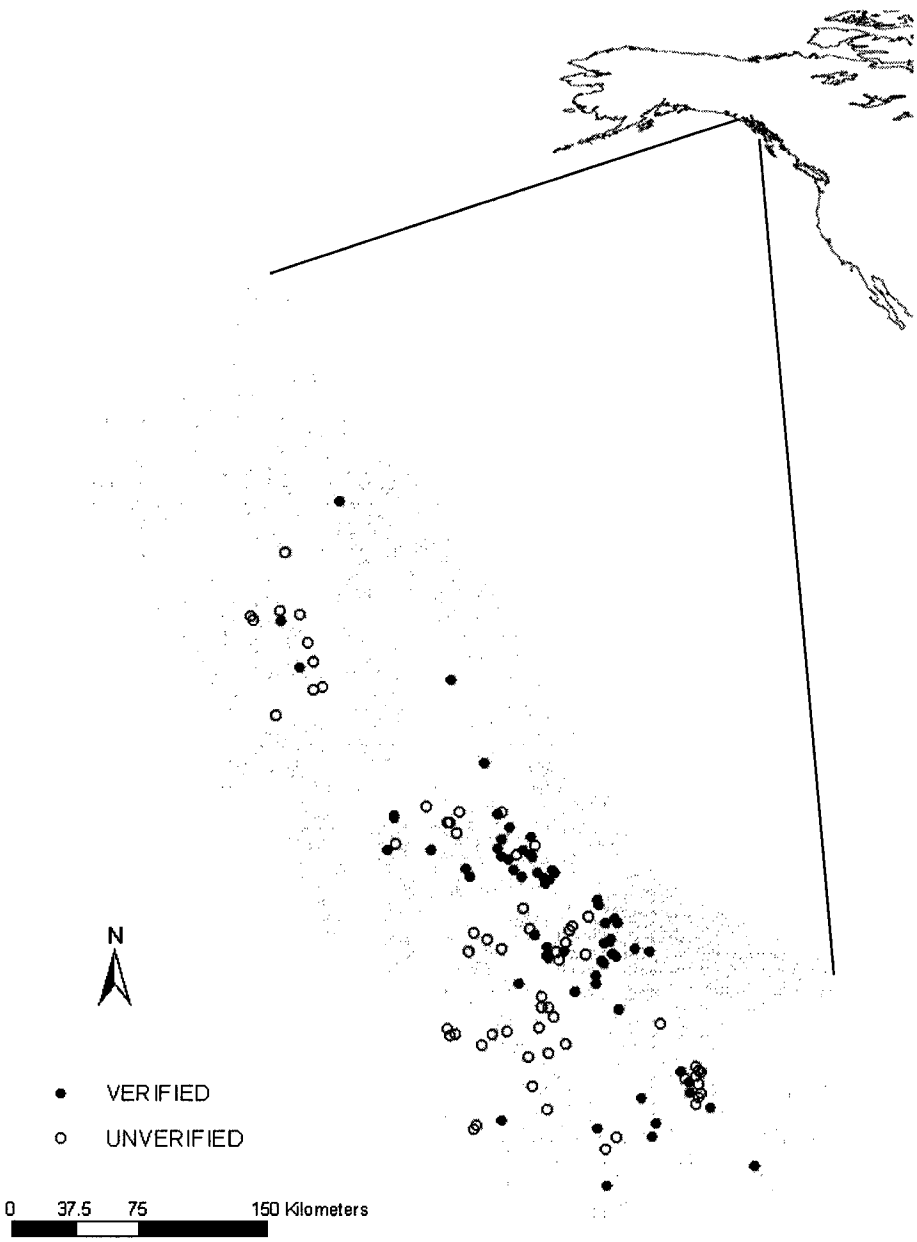

Figure 4.1. Sites sampled for fish species presence in the Alexander Archipelago and mainland coast of southeastern Alaska (55°N to 58°N). Solid circles are sites where presence or absence was conclusively established; open circles were unverified reports.

Figure 4.2. Upstream movement barrier.

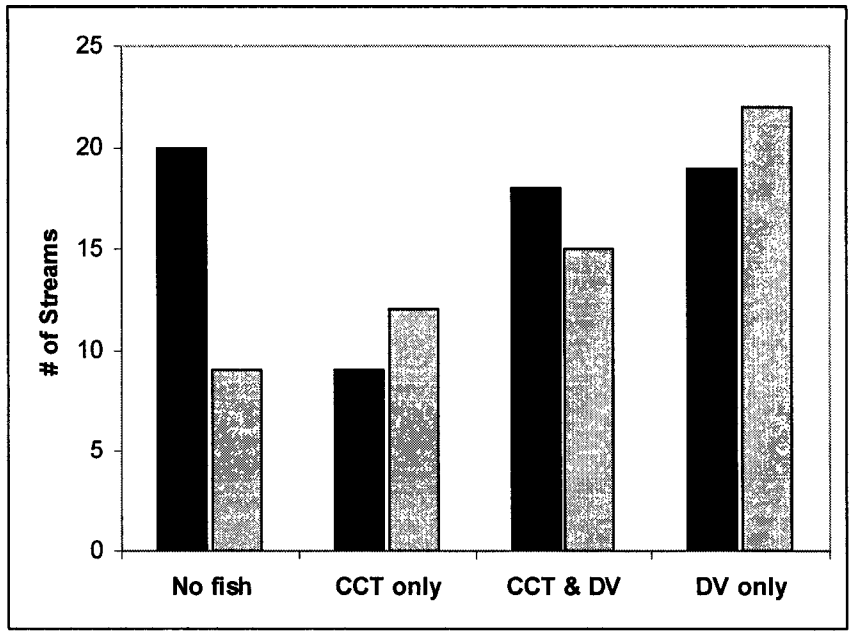

Figure 4.3. Comparison of isolated streams in our verified (dark bars) and unverified (light bars) datasets. The relative distribution of streams where coastal cutthroat trout (CCT) and/or Dolly Varden (DV) were found is similar for the two datasets, and is representative of all streams in the region with isolated populations of these species. Only the numbers of fishless streams are not representative, a result of deliberate sampling bias in the verified dataset and of rigorous screening of many allegedly fishless streams from the unverified dataset.

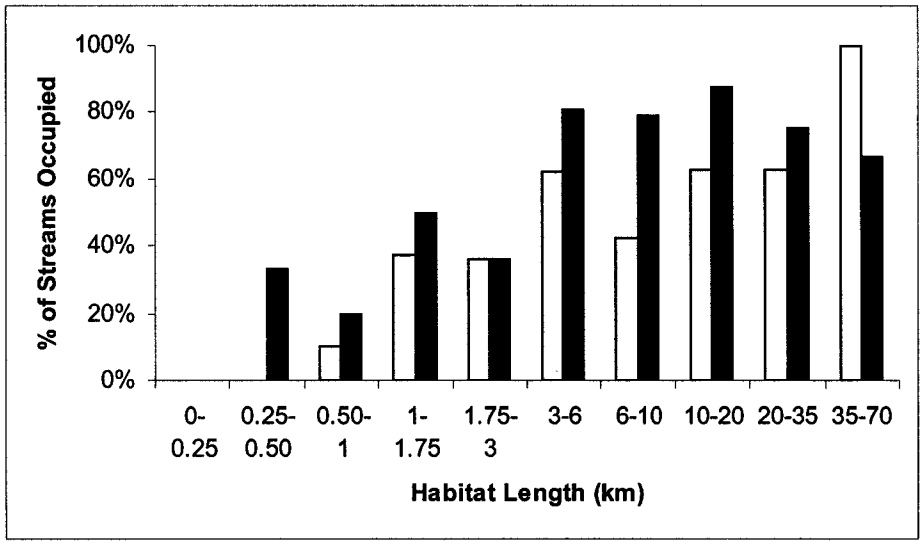

Figure 4.4. Percentage of streams of various lengths where isolated populations of cutthroat trout (light bars) and Dolly Varden (dark bars) were found. The x-axis is logarithmic to highlight data for streams near the presence-absence threshold. The width of each habitat length stratum is approximately the same on a logarithmic scale, but not all strata contained an equal number of streams. The number of streams/stratum varied from 3 in the two outermost strata to 22 in the central strata where our sampling effort was concentrated.

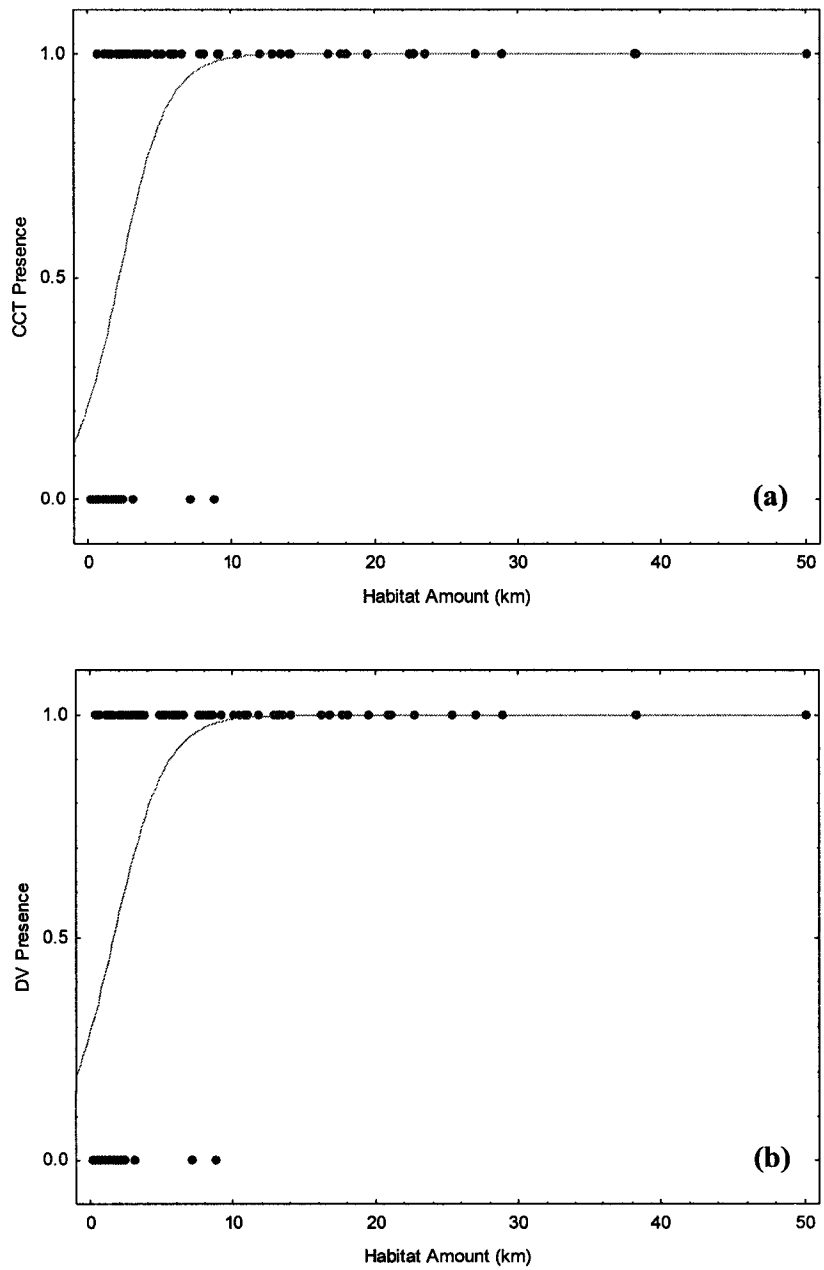

Figure 4.5. Fitted logistic regression curves, with presence-absence data, for isolated populations of (a) coastal cutthroat trout, and (b) Dolly Varden. The three outlier sites (longer streams) where no fish were detected are from our unverified dataset, and may in fact contain fish.

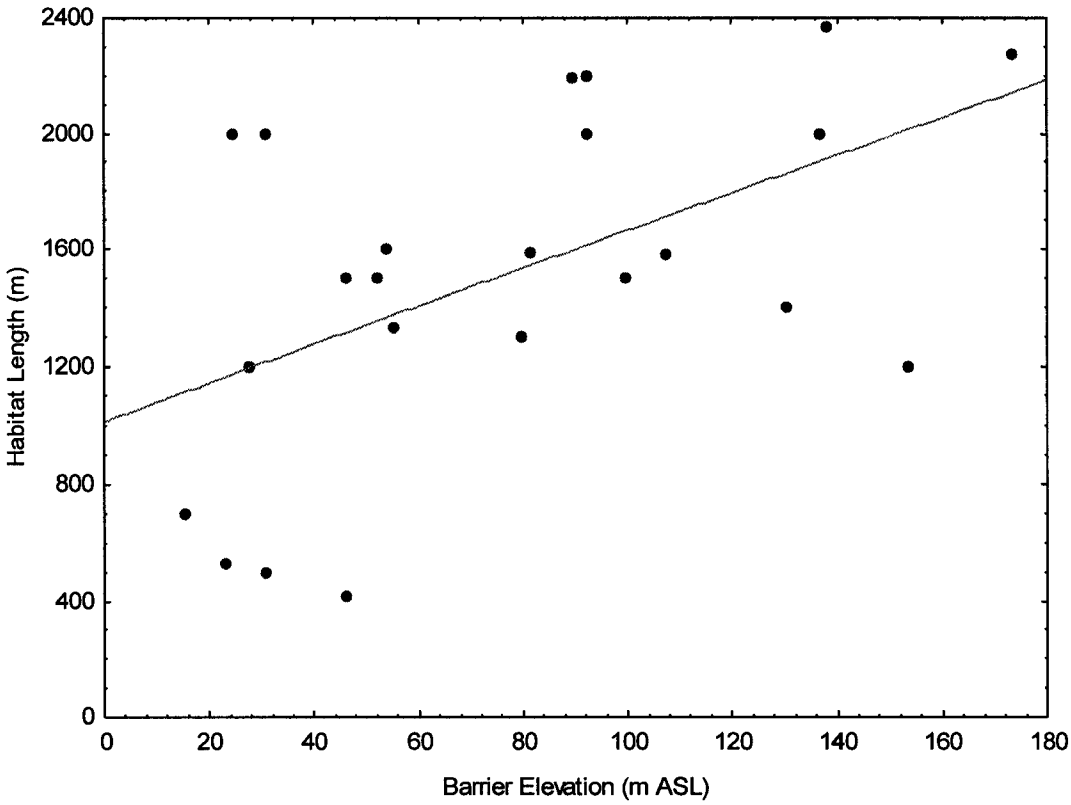

Figure 4.6. Fish presence in isolated stream reaches as a function of both habitat length and elevation at the top of the upstream movement barrier. Dots represent the lower quartile of streams with fish present above barriers (streams with less than 2400 m of habitat). The amount of habitat in smaller streams where fish were present is positively correlated ($r = .52$, $p = .01$) with barrier elevation, a surrogate for isolation period. The correlation between habitat length and elevation for the set of all sampled streams less than 2400 m long was not significant ($r = .19$, $p = .19$), indicating that the relationship between habitat requirements and isolation period is not merely a sampling artifact.

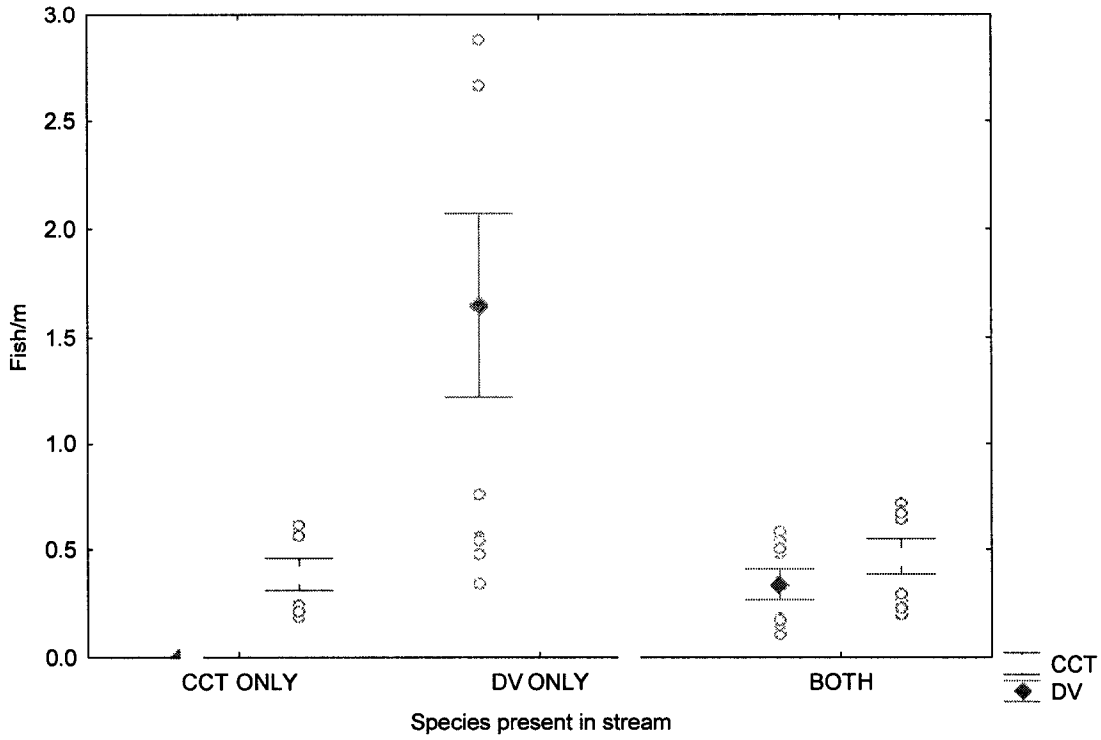

Figure 4.7. Density of coastal cutthroat trout (CCT) and Dolly Varden (DV) where they occur together in headwater streams (n=12) or alone (n=4 for CCT and n=7 for DV). Streams were sampled annually for 2-6 years (median=4). Whiskers indicate 95% confidence interval; open circles are outliers.

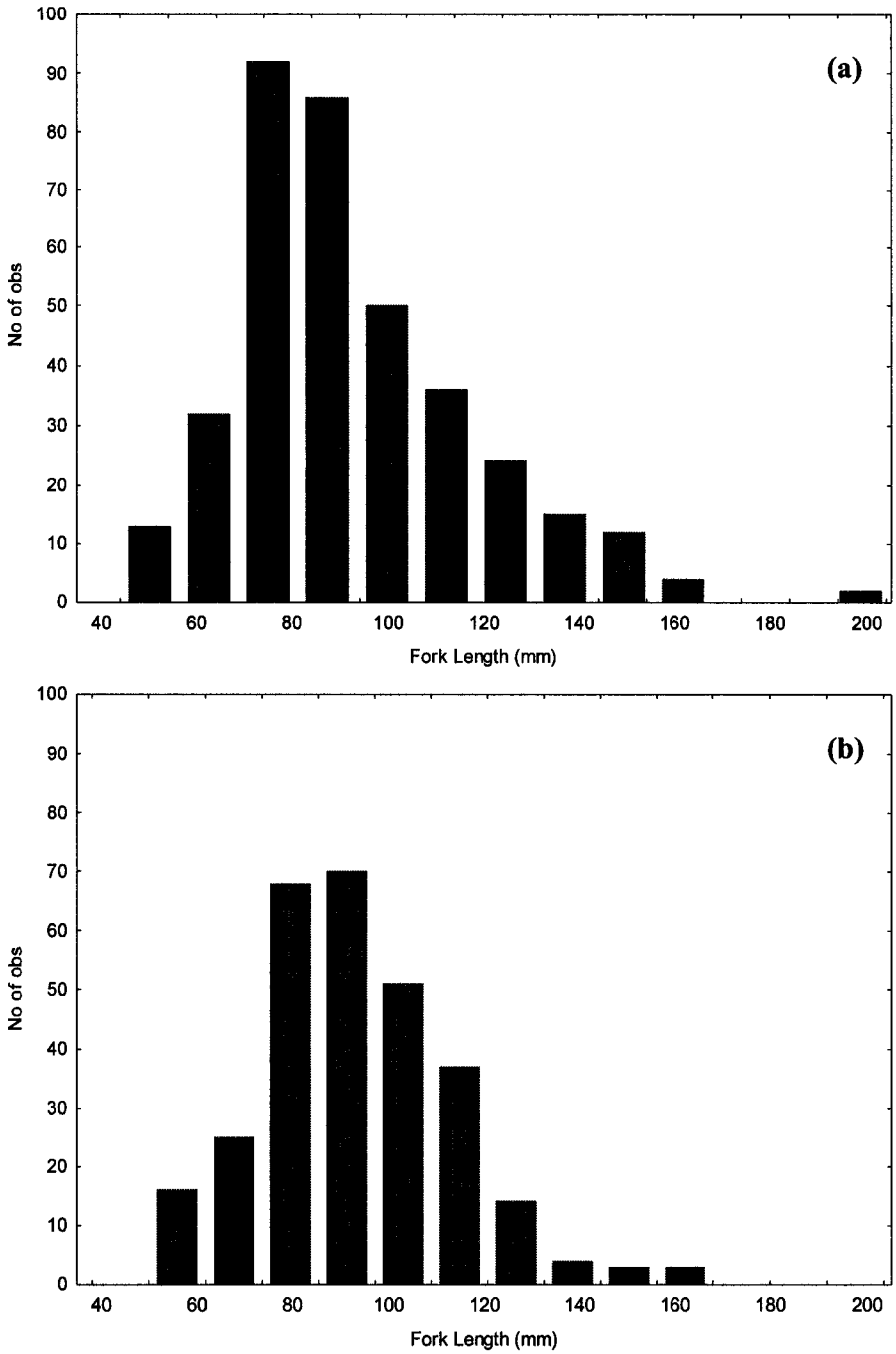

Figure 4.8. Length frequency distributions of representative isolated, stream-resident populations of (a) coastal cutthroat trout (n = 366), and (b) Dolly Varden (n = 291) from southeastern Alaska. Fish were sampled by minnow trap during the summer of 2004.

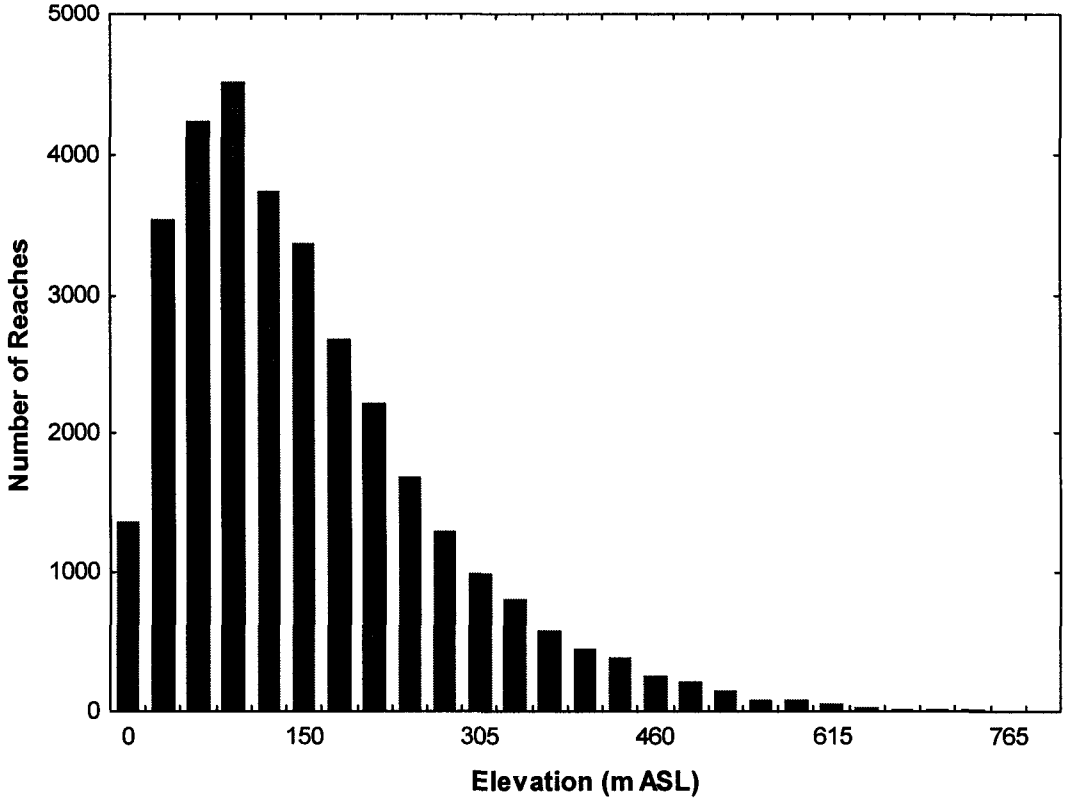

Figure 4.9. Distribution of all resident fish stream reaches by elevation for the entire study area (source: Tongass National Forest GIS "streams" layer, January 2005).

CHAPTER 5 –Evaluating the Effectiveness of a Large, Distributed Reserve Network

ABSTRACT

In parts of the world where significant numbers of native species and their habitat still persist, reserves are often set aside to buffer the biota from the progressive effects of development. Setting aside land for reserves is costly, and there is considerable interest in monitoring the results, following the adaptive management paradigm. But the design of large-scale programs to monitor species and habitat status is still in its infancy. The complexity of large ecosystems and the open-ended nature of monitoring often conspire to produce grandiose monitoring plans that fail to deliver, and sometimes even fail to be implemented. We use the recently adopted conservation strategy for the Tongass National Forest in southeastern Alaska as a case study to explore a different approach to developing a monitoring program for a large-scale conservation strategy. Central to our approach is an operational framework that allows monitoring components to be added and deleted over time, keeping the size of the monitoring program matched to available resources and providing the flexibility to close out issues that are settled and address new ones as they emerge. We propose a larger role for research scientists to provide the integration of results that would otherwise be directly encoded in the design of a monolithic but static monitoring program, and to translate scientific conclusions into management recommendations and so that the tantalizing potential of the adaptive management paradigm might actually be realized.

INTRODUCTION

A common conservation strategy is to designate a network of protected habitat reserves in embedded in a landscape that is otherwise open to development (Noss & Cooperrider 1994; Soule & Terborgh 1999). Putting entire landscapes into reserve status is usually impractical, and for wide-ranging species such as wolves, tigers, and whales that will make use of inferior habitat at least part of the time it is also probably unnecessary (Margules & Pressey 2000; Poiani et al. 2000). The challenge is to determine how much and which parts of a landscape should be held as reserves in order to maintain viable populations of all target species. Whether it be national parks in Africa or marine reserves in the South Pacific, there will always be a tension between the desire to develop some areas for direct human benefit and to maintain others in an undeveloped status for the maintenance of biodiversity. Those who argue in favor of landscape-scale reserve networks are under pressure to show that the number and arrangement of reserves are both necessary and sufficient to meet conservation goals.

It is not possible to know in advance whether a reserve network will "work". Real-time evaluation of the effectiveness of large, distributed reserve systems is important if they are to receive continued support in the face of increasing development pressure and it is also needed to guide refinement of reserve network designs, using the adaptive management paradigm (Johnson 1999; Walters & Cahoon 1990). Yet the challenge is formidable. Reserve networks are usually intended to conserve multiple species, particularly species with long life spans and naturally low reproductive rates for which detecting significant population trends is a protracted exercise. Target species may not be evenly distributed across the reserve network; some reserves may be more

important for some species than for others. A reliance on the indicator species approach is fraught with opportunities to miss the effects of subtle but significant differences in how individual species or even populations are affected by habitat changes (Landres et al. 1988; Niemi et al. 1997). Selecting and measuring variables that reflect the status of target species is only the first hurdle.

Reserve networks encompass much larger areas than the spatial extent of typical scientific investigations, making the logistics of evaluating them a major challenge. In addition, reserve networks tend to be developed progressively, so that the "treatment" being evaluated is not static. Furthermore, there is typically little or no regulation of what happens to that part of the landscape that is not in reserve status, the so-called matrix lands (Franklin 1993). In one part of a reserve network, the matrix may be largely undeveloped and approach the habitat value of a reserve, whereas in another part, or perhaps at a later time, the matrix may be developed and have little habitat value or, worse yet, function as a barrier or population sink. The spatial extent of reserve networks and complex spatiotemporal variation within them makes controlling for unwanted variation across the study a second major challenge.

Finally, the evaluation of conservation strategies is seen as "effectiveness monitoring", an activity perceived by many scientists as uninteresting. Effectiveness monitoring is typically left to the resource managers who design those conservation strategies. Conducting scientific inquiry in the context of the problems mentioned above calls for creative approaches, sophisticated study designs and data analyses, and multidisciplinary teams. Yet scientists working for government land management agencies such as the United States Forest Service and non-governmental conservation

organizations such as The Nature Conservancy are often relatively isolated, both from each other and from their peers in academia, as well as from the creative thinking and sophisticated techniques that are presented at scientific meetings and seminars. They face limited access to scientific literature, colleagues, training, new knowledge, and also to funding sources that target scientific researchers. This reduction in the size of the toolkit available to many of those charged with evaluating the effectiveness of distributed reserve networks is a third major challenge.

We offer a proposal for an operational framework to guide the evaluation of the reserve-based conservation strategy recently adopted for the Tongass National Forest in southeastern Alaska. We propose a set of key components for the monitoring program, and a flexible approach that allows the components to evolve in response to changing information needs and opportunities. We emphasize the need for greater participation by research scientists at multiple stages of the process, and we describe some of the benefits of this approach, not only for policy makers but for the researchers as well.

TONGASS NATIONAL FOREST CONSERVATION STRATEGY

The Tongass National Forest is by far the largest National Forest in the United States, essentially comprising an entire ecoregion, the Pacific Gulf Coastal Forest-Meadow province (Bailey 1995; Nowacki et al. 2001). The boundaries of the Tongass include almost the entire panhandle of southeastern Alaska, essentially the entire Alexander Archipelago and associated mainland coast. The Archipelago covers approximately 500 km of latitude and 150 km of longitude, and it includes over 22,000 islands (USDA Forest Service 1997). It is bounded on the west by the open Pacific

Ocean and on the east by a nearly unbroken range of mountains. North of the Archipelago, the rocky coastline comes to an end and is replaced by sweeping sandy beaches. To the south, the Archipelago stops at Dixon Entrance, a broad body of water that approximates the location of an ecotone representing the northern limit of a number of terrestrial species.

The Alexander Archipelago is steep, rugged terrain partitioned by deep fjords, with a temperate rainforest climate dominated by the frequent arrival of storms off the North Pacific. The naturally fragmented landscape harbors an especially high percentage of endemic species and subspecies (Cook et al. 2001; Smith *in press*). While there is concern about the long-term viability of some wildlife species and populations, none are presently considered to be actually hovering on the brink of extinction, and many parts of the landscape remain relatively undisturbed by anthropogenic influences. However, commercial logging and associated road building have affected a large portion of the Tongass (Durbin 1999), and these activities continue to expand. Except on private lands, logging and road building are governed by the Tongass Land Management Plan (henceforth "TLMP"), most recently revised in 1997 (USDA Forest Service 1997). Unlike many other National Forests, federal land ownership in the Tongass is largely continuous, with only a few inholdings belonging to the state and to Alaska Native corporations. Except for these few, large tracts and an equally small number of urban areas, nearly all land development activities in southeastern Alaska are governed by the provisions of TLMP.

A conservation strategy for the Tongass National Forest is laid out in TLMP. The broad goal of the strategy is, in accordance with the National Forest Management Act, to

maintain viable populations of all native and desired non-native species, well-distributed across the landscape (USDA Forest Service 1982). The TLMP conservation strategy includes both a coarse filter reserve network approach intended to benefit all species and fine filter provisions that further address unique needs of particular species. The coarse filter approach comprises a set of roughly circular reserves, along with narrower strips of protected forest that buffer all significant streams as well as all freshwater and saltwater shorelines. These buffer strips are expected to provide some degree of connectivity between reserves, although they were not explicitly laid out to achieve this goal. Reserves are more or less evenly distributed across the entire Tongass and are protected for the life of the forest plan from most further development activities. (However, portions of many reserves have experienced past logging and roading, since it was impossible in 1997 to specify a reserve network that avoided all previous development).

Fine filter provisions in the TLMP conservation strategy focus on unique habitat requirements of individual species, most often carnivores. Wolf dens and goshawk nests outside of reserves are buffered from development activities. Additional trees and snags are left standing after timber harvest in areas where habitat for American marten has previously been impacted. Riparian zones where brown bears forage for salmon are protected from development. These fine filter provisions were included where scientists felt that the coarse filter reserve strategy could be insufficient to maintain well-distributed viable populations of particular species. In most cases, the fine filter provisions were scientifically motivated (e.g. martens do best in intact forest with plentiful snagsBuskirk & Powell 1994), but the specific details of the provisions were educated guesses (*e.g.* 3

large snags left standing per acre) . Implementation of fine filter provisions still leaves much to the judgment of forest managers (*e.g.* the pattern of snag distribution).

Development of the TLMP conservation strategy was largely driven by concerns about the continued viability of large wildlife species thought to be dependent, at least in part, on the presence of large tracts of old-growth forest. Early in the forest plan revision process, an interagency committee was charged with developing a strategy that would address such concerns. (A separate concern for the maintenance of fish habitat, particularly for the salmon that are a mainstay of the region's economy and culture, had earlier led to the designation of riparian buffer strips along all fish streams in the Tongass Timber Reform Act of 1990.) The so-called Viable Populations Committee ("VPOP") took the approach of identifying a set of old-growth associated species that were deemed especially vulnerable because of threats to their habitat, life history traits, or their population structure, hereafter referred to as the conservation strategy "design species". The overall strategy proposed by the VPOP Committee was the union of all of the protective measures deemed necessary to ensure continued viability for each of the nine design species (Suring et al. 1993). The species-based approach selected for the development of the conservation strategy would later lead the Tongass National Forest to take a species-based approach to the evaluation of its effectiveness.

The conservation strategy proposed by the VPOP Committee was submitted for review by research scientists from 18 institutions outside of Alaska (Kiester & Eckhardt 1994). Reviewers were especially concerned about the small number of design species, the limited amount on information available about the status and habitat requirements of those design species, and the limitations of a species-based approach. Attention was also

drawn to the high degree of population structuring induced by the naturally fragmented island landscape of the Tongass. These concerns were acknowledged in a formal response by the VPOP Committee (Suring et al. 1994), but the strategy remained largely unchanged.

In 1993 and 1994, petitions were filed to list as endangered two wide-ranging predators found in the Tongass: the Alexander Archipelago wolf (*Canis lupus ligoni*) and the Queen Charlotte goshawk (*Accipiter gentilis laingi*) (U.S. Fish and Wildlife Service 1994a, b). Conservation assessments for these two species were prepared (Iverson et al. 1996; Person et al. 1996), further focusing conservation concerns on individual species. The goshawk was designated a "sensitive species" by the Forest Service and became an additional *de facto* design species for the conservation strategy; the wolf had already been identified as one by the VPOP Committee. When TLMP was ultimately adopted in 1997, the U.S. Fish and Wildlife Service relied in large part on the protections imposed by the TLMP conservation strategy to deny a designation of threatened status (U.S. Fish and Wildlife Service 1997a, b).

Because of the large size of the Tongass, the high public interest in ensuring maintenance of its biodiversity, and the fact that the Tongass was the first National Forest to undertake a forest plan revision under the regulations of the National Forest Management Act, the Forest Service pioneered a new approach to incorporating the scientific perspective in Tongass policy development (Everest *in press;* Mills et al. 1998). Research scientists from the Forest Service's Pacific Northwest Research Station were included as full members of the planning team, charged with developing a scientific analysis of the predicted effects of various policy alternatives. Scientist team members

oversaw a panel assessment process to further review the proposed conservation strategy for the Tongass, along with other key components of TLMP (Shaw 1999). Panel assessments were focused especially on viability concerns in areas where old-growth habitat had already been substantially reduced, and on the protection of small populations of island endemics. The former concern resulted in a guideline that called for future timber harvests to leave a significant percentage of stand structure in place (large trees, snags, and downed logs) in areas where more than a third of the original old-growth had already been harvested. The latter concern resulted in a provision that put all islands under 1000 acres off limits to harvest. Multiyear studies were also initiated to explore a few priority information needs, including the distribution of endemic mammals, impacts of clearcutting on riparian zones and forested wetlands, and ecological effects of alternative harvest methods (USFS 1997: Appendix B; results of these studies will be published in a special issue of Landscape and Urban Planning in 2005).

The Tongass conservation strategy was a bold application of largely untested assumptions about the effect of habitat on population dynamics. The influence of scientific perspective was evident not only in the provisions of the conservation strategy but in the extensive analysis developed to support it, but the job of evaluating the strategy still lay ahead. When TLMP was signed in 1997, it included a skeletal monitoring and evaluation plan that identified key monitoring questions for resources such as fish and wildlife, as well as for other social and economic resource areas (USFS 1997: Chapter 6). The monitoring plan specified a continuing role for Forest Service research scientists in developing, implementing, analyzing, and interpreting effectiveness and validation studies. It also left much unspecified, and where details were provided they were later

often deemed to be inappropriate or inadequate. For instance, trends in some wildlife species were to be evaluated using harvest statistics, a notoriously biased sampling regimen (Strickland et al. 1996). No wildlife habitat monitoring was specified, except in the so-called "biodiversity" monitoring protocol which consisted of nothing more than evaluating changes in the total amount of a handful of forest cover types at a very coarse spatial resolution, based on a database of unknown and inconsistent accuracy. Still more problematic was the lack of a formal adaptive management framework for tying specific monitoring objectives to the resolution of scientific uncertainties that undermined confidence in the new TLMP.

An interagency advisory group was convened in 1997 to assist the Forest Service with developing and implementing its monitoring plan. Seven years later, a number of monitoring protocols have yet to be finalized. With the exception of several studies independently conducted by the Pacific Northwest Research Station (*e.g.* Bryant et al. *in press;* Woodsmith et al. *in press*), almost none of the monitoring data that has been collected has been analyzed in such a way that results could provide feedback to the policy development process. Several attempts have been made to develop a conceptual framework for the monitoring program to address this concern by better integrating its components, and ensuring that the highest priority monitoring tasks are getting done (Alaska Department of Fish and Game 2001; Smith *in prep.*), but none have yet been generally adopted. In what follows, we attempt to build on these efforts, and we specifically address the role of research scientists in helping achieve monitoring program goals.

AN OPERATIONAL FRAMEWORK FOR EVALUATING THE STRATEGY

Conventionally, monitoring activities are broken into four categories: baseline monitoring; implementation monitoring, effectiveness monitoring, and validation monitoring (Noss & Cooperrider 1994). From the scientific standpoint, these activities range from the fairly routine (verifying the accurate implementation of a resource management policy) to potentially quite challenging (testing fundamental assumptions about ecosystem processes). A complete monitoring program will include the full range of activities, carried out by participants with widely differing amounts of experience. Later, we will expound in more detail on monitoring program components and the roles of participants, especially research scientists, but first we argue that *all* components of a monitoring program must follow some common ground rules that recognize the basic scientific nature of the enterprise.

Monitoring *per se* consists of data gathering. Competent data management and data quality assurance procedures are required if scribbles on a page or numbers in a spreadsheet are to be transformed into usable data (Palmer 2003). Data management and storage is a formidable task and one often given inadequate attention by people who have not previously worked with large quantities of data that are collected by more than one individual or team. On any large project, all monitoring data need to be stored in a central repository in a common, documented format (Michener et al. 1997). It's a simple enough principle, but one rarely followed to the letter. A noteworthy exception is the National Science Foundation's LTER program (Hobbie et al. 2003), which has invested considerable energy in the standardization of data management techniques (Michener et al. 1998).

Data quality control and quality assurance are additional concerns. Data quality measures include both specifying procedures that minimize observer bias during data collection as well as implementing procedures to detect corrupt data after collection (*e.g.* due to transcription errors). The U.S. Environmental Protection Agency is a particularly good resource for guidance on the development of data quality control and quality assurance (U.S. Environmental Protection Agency 2002). Individual monitoring activities will differ in the level of data quality needed, but all monitoring activities will benefit from the thought exercise of developing a data quality plan.

That said, the key to approaching the evaluation of a comprehensive, landscape-scale conservation strategy is acceptance that this broad objective is neither a single question nor one that can ever be comprehensively and finally answered. The area involved is too vast and diverse for a representative sampling scheme to be both meaningful and logistically feasible. The potential numbers of significant explanatory and response variables are both enormous, and their values wide-ranging. Either controlling for or analyzing the numerous interactions between them across an entire region is impossibly challenging. In this context, an operational framework is needed to provide guidelines for determining which parts of the evaluation to tackle first, and at what resolution (Atkinson et al. 2004; Schoonmaker & Luscombe 2005).

While such decisions will often be carefully thought out, others may be opportunistic. When grappling with intractable problems, any opportunity that helps to gain a toehold may be worth considering. For instance, the appointment of a new faculty member may add expertise that was not previously available, perhaps in modeling, population ecology, or remote sensing. Similarly, the development of a new technique or

new technology may transform an intractable problem into one more amenable to investigation. A commonly agreed-upon operational framework helps keep the focus on the main questions while allowing the monitoring program to evolve in response to new information and changes in funding levels and resources. At the same time, an operational framework helps policy makers assimilate new monitoring data by placing them in the context of the overall monitoring objectives.

Components of the Operational Framework

For the evaluation of a large, distributed reserve system such as that described by the Tongass conservation strategy, we propose an operational framework with four components: (1) implementation monitoring; (2) periodic state-of-the-ecosystem assessments; (3) evaluations of specific management practices; and (4) tests of policy assumptions about ecological processes. None of these components alone can address evaluation of the *overall* reserve system and its myriad objectives, but experience has shown this grand goal to be unattainable due both to ecosystem complexity and to logistical and financial constraints (the monitoring program for the Northwest Forest Plan, which evaluates only seven natural resource components, costs over $6,000,000 annually; USDA Forest Service 2002b). In addition, monolithic monitoring designs are difficult to adapt when new ecological concerns or management information needs are identified (Ringold et al. 1996). The reality of working in a resource management context is that policy decisions must frequently be made long before scientific questions have been answered with a research scientist's desired level of certainty (Nyberg & Taylor 1995), and interesting lines of scientific inquiry must often be abandoned and

others initiated at more frequent intervals than most researchers would prefer. The operational framework that we propose breaks the problem down into smaller pieces to facilitate the necessary flexibility, and to provide distinct and complementary roles for biologists working in both agency and academic contexts. It attempts to resolve the need for compiling long-term monitoring datasets with the reality of ongoing changes in both the policy and the ecosystem being evaluated.

Component 1: Implementation Monitoring

Implementation monitoring is simply the act of checking to see that the policy was indeed implemented as planned. Without implementation monitoring, it is impossible to know whether the written policy is actually what is being evaluated by the remainder of the monitoring program. For the Tongass conservation strategy, implementation monitoring would include answering questions like: if reserves are supposed to be of a certain minimum size, are they indeed that large? If buffers are supposed to be of a certain minimum width, are they indeed that width? Some questions about implementation can be grayer, especially where policy guidelines are not quantitative but qualitative. For example, in the Tongass extra-wide forested buffer strips are supposed to be left along each stream bank along reaches important to brown bears foraging for salmon. Measuring the width of a buffer is easy enough, but determining which stream reaches are important foraging sites for bears, and thus require those additional buffers, is more problematical. The design of an implementation monitoring program, in addition to helping ensure policies are implemented as planned, also brings to attention points such as this where policy clarifications are needed. Importantly, an

implementation monitoring program loses much of its credibility if some measure of third-party oversight is not included (Bella 1997).

Component 2: Inventories and Assessments

Second, some knowledge of the state of the ecosystem and its components are needed. Prior to the invention of GIS, this information generally consisted of inventories of species present. A simple list of species is a good starting point, but because species are not continuously distributed across a region, it is also important to know something of the intra-regional distribution of each species. For species whose distribution is discontinuous – which for islands in the Tongass would include almost all terrestrial species, as well as many aquatic ones – distribution maps can also help to suggest the number and sizes of distinct populations that may be present. It is important to maintain not only viable populations of all species, but their distribution as well, as acknowledged by the National Forest Management Act (USDA Forest Service 1982).

In addition to inventorying species and mapping their distributions, it is also desirable to map habitat types and their distributions. "Habitat types" can be a problematic concept, since habitat is in the eye of the beholder. For each species, a map of the different types of habitats within its range will look different. Thus, it is best, at least at a coarse level of resolution, to consider habitat value a consequence of physical processes such as geology and climate, and classify landscapes according to the interaction of these processes, as Nowacki et al (2001) have done in their definition of ecological subsections for the Tongass, at a resolution of about 25-2,500 km^2. Habitat values at a finer resolution are a result as well of vegetation structure and diversity. The

Tongass has developed a number of classification schemes to capture both physical and biological variation at this scale. These include classifications motivated by geomorphology (landforms, stream channel types), geology (parent rock, soil type), and vegetation (plant association, forest stand structure). Resolution (minimum map unit size) for these classifications is on the order of 0.25 km^2 for terrestrial classes, or 0.1 km for linear stream channel types. Not all of the Tongass has been completely classified for each scheme, but the classification that exists is extensive and illuminating for ecologists (Brock et al. 1996; Pawuk & Kissinger 1989; USDA Forest Service 1992).

Many of these maps will be static over a period of decades or more. Landforms, soil types, and the like do not generally change during the lifespan of a typical monitoring program, and they need be mapped only once to provide explanatory context for more dynamic processes. However, a monitoring program should also include periodic remapping of habitat features that do change over on a temporal scale comparable to that of the evolution of resource management policy. For adaptive management to work, the feedback loop from monitoring results to suggested policy adjustments must occur fairly rapidly (Bormann 1994). Management plans for individual forests like the Tongass are revised every 10-15 years (USDA Forest Service 1982). For the most part, forest management policy can only be amended when the revision window is open, and since forest plans are amended every decade or so, the policy that is being monitored changes significantly at that point.

The key is to identify habitat features that are potentially altered by development activities. In the Tongass, road building and timber harvest are the predominant development activities, although there are also a few sites where urbanization, intensive

recreation and tourism, and mineral extraction are influential. Road construction can result in aquatic organism passage problems at stream crossings, erosion, runoff, and increased human presence, among other impacts (Trombulak & Frissell 2000). Roads may also either deter or concentrate animal movements. Timber harvest alters vegetation composition and structure and may cause erosion. Like road construction, timber harvest may alter wildlife spatiotemporal use patterns in a variety of ways. Changes that should be periodically remapped include:

- Vegetation composition and structure: Habitat value may be dependent on both forest stand structure and the nutrients present in vegetation.
- Road network: Information about when road segments were constructed and maintained should be included, as well as the status of any road-stream crossings.
- Soil movement: This category includes landslides and erosion, both of natural and of anthropogenic origin.
- Human concentrations: Recreation sites, mines, towns (with boundaries and approximate numbers of people present during summer and winter).
- Wildlife concentrations: High use areas and den sites should be mapped both by species and by season (*e.g.* stream reaches where bears congregate to forage for fish during the salmon spawning season). Where conflicts with specific local human activities are a concern, it may also be worth differentiating wildlife presence at different parts of the day.

Component 3: Effectiveness of Specific Management Practices

The third component of our proposal is the evaluation of specific management practices. It is somewhat more feasible to evaluate the direct effects of a single type of treatment than it is to evaluate the effectiveness of a multidimensional conservation strategy, although there always remains the problem of choosing a design that adequately controls for background variation. The effort is important, however, as most individual components of the conservation strategy are costly to implement, at least in the sense of lost opportunity costs, and there will be significant pressure to drop them if they are not demonstrably contributing to conservation goals. Management practices chosen for evaluation should be those that are most costly to implement, that are thought to contribute the most to conservation, and whose efficacy is the least certain.

For the Tongass conservation strategy, examples of specific management prescriptions would include particular buffer widths, requirements for snags and live trees left in harvested stands, and avoidance of nest or den sites while they are occupied. Not all management practices can be evaluated directly, and it is important not to waste valuable monitoring resources collecting data that cannot be analyzed in a statistically valid manner to evaluate the practice in question. One of the biggest challenges to evaluating the effectiveness of specific management prescriptions is matching the scale of the prescription to that of the response variable. For instance, if a certain amount of vegetation structure is to be left standing for wildlife habitat after timber harvest, it is difficult to evaluate how this impacts organisms whose typical movement area is much larger than the harvested stand. The post-harvest success or failure of an organism may be tied to habitat quality within the harvest unit, or it may be entirely driven by conditions in the surrounding landscape. For this reason, tests of specific management

practices should ideally be conducted where the practice is consistently applied over an area at least as large as the area used by the organism being monitored. An example from the Tongass would be a smaller island where the entire island was harvested according to a consistent policy, be it clearcutting or some form of partial cutting or second growth treatment. Not only are such situations relatively rare, but it is even more rare that they are replicated at a suitable scale.

An alternative approach is to use a before-after study design. Several years of data are collected before the treatment is applied, and data collected after treatment application are compared with pre-treatment data. One of the biggest challenges with using this design in a management context is that planned treatments are not always implemented. Lawsuits frequently alter the timing of timber sales and sometimes result in their cancellation, turning the pre-treatment data into control data and leaving the researcher without any post-treatment data at all. One way to accommodate this uncertainty is to establish a number of pre-treatment sites on the assumption that at least some will be treated and the others will remain as controls. This is effectively the before-after-control-impact (BACI) design, although the designation of control sites is not done in advance but a result of the vagaries of the forest plan implementation process. This was the design chosen by the Tongass for monitoring the impacts of timber harvest on resident fish indicator species (USDA Forest Service 2000).

In order to evaluate the effectiveness of a specific management practice, it is essential to define precisely how effectiveness will be measured and scored. We have observed a tendency on the part of managers to conclude that because no problems were detected after the application of a management treatment, the treatment must have been

effective. With this attitude, the risk of making type II errors is high. Before it can be concluded that no problems occurred, the monitoring protocol used must be evaluated for its power to detect specific negative outcomes (Steidl et al. 1997; Taylor & Gerrodette 1993).

Effectiveness can be defined by either a positive or negative threshold for some clearly defined measurable quantity, such as level of dissolved oxygen in stream water (positive) or the suspended sediment load (negative). However, most response variables are not static, and it will typically be necessary to make repeated measurements of the response variable over a long period of time to ensure that a moment of "effectiveness" is not bracketed by less desirable conditions. A management practice may be deemed effective immediately after it is applied, but this could be misleading if the negative effects of that practice take time to manifest themselves. A good illustration of this concept is the response of understory vegetation to clearcut harvest (Alaback 1982; Oliver & Larson 1996). Initially, the understory responds to the increased sunlight with a flush of vegetation. If the desired result is a flourishing shrub layer to provide forage for ungulates, clearcutting appears quite effective. But after several decades, a new cohort of trees begins to block light from reaching the understory, and if measurements are made at that time, clearcutting would appear very ineffective for maintaining a thriving shrub layer. The effectiveness of other practices may be discernable only if measurements are taken at the correct time. Otherwise, the practices might appear to be neutral. An example of this would be forested buffer strips left along high gradient streams to control erosion of the stream banks. If erosion only occurs during a major event such as a 100

year storm, then it would be misleading to measure erosion rates after lesser storms and conclude that the buffer is effective if no erosion is detected.

The Tongass fish and wildlife monitoring program developed by the Forest Service has relied mainly on the indicator species approach, choosing certain populations of certain species to monitor over time. The use of indicator species to evaluate the effectiveness of resource management policies has been much debated (Caro & O'Doherty 1999; Landres et al. 1988; Simberloff 1998; Weaver 1995), and has been a focal point of efforts to revise the planning rule for the National Forest Management Act (USDA Forest Service 1999, 2002a). In general, we do not believe that the indicator species approach is a fruitful one for the Tongass. Above and beyond the problem of choosing an indicator species whose status meaningfully reflects the status of other species, there are concerns about lags in response time for long-lived species (which includes many wildlife species when compared with the 10-15 year lifespan of National Forest management plans) and, especially in the Tongass, the difficulty of collecting demographic information about any wildlife population and the large number of putative populations inhabiting islands with diverse management impacts. An earlier effort to develop a conceptual framework for evaluating the effectiveness of the Tongass conservation strategy recommended broadening the wildlife monitoring program to include more than just the species-based approach that is more or less mandated by the existing regulations for the National Forest Management Act (Alaska Department of Fish and Game 2001).

Component 4: Tests of Assumptions

An effective monitoring program for a multifaceted conservation strategy that covers as large and complex an ecosystem as the Tongass involves more than just looking for trends in periodically repeated inventories and testing individual management practices. The strategy rests on the acceptance of many untested assumptions about habitat relationships, demography, and population structure. A proactive approach to evaluating the strategy will also include a parallel track of testing critical assumptions, the fourth component of our proposed operational framework. This component is often referred to as validation monitoring, that is, "monitoring" conducted with the goal of validating the assumptions that underlie policy. We find the term "validation monitoring" to be unfortunate. Research that is conducted merely to validate generally accepted assumptions is usually much less interesting than research that strives to evaluate debatable assumptions. Furthermore, evaluating assumptions is very nearly basic research, and calling it monitoring discourages researchers from becoming involved. To many researchers, monitoring implies little more than repeated collection of generic data continuing indefinitely into the future, with little attention paid to how the data might be used.

On the contrary, exploring untested assumptions is the very stuff of scientific research. Within the broad confines of the generalized information needs identified by agency personnel, there is more than adequate room for basic research on ecological processes. Resource managers are sometimes reluctant to provide researchers with the license to follow their interests in unanticipated directions as research progresses, but we believe that such freedom is beneficial and necessary for both parties. A well-crafted

resource management policy should already have incorporated the best available scientific advice. Only by supporting research in *unexplored* territory are policy makers likely to gain significant new insights about previously unconsidered weaknesses in the policy. The serendipity that is responsible for so many scientific breakthroughs can also increase the likelihood of policy breakthroughs.

Example: Headwater Stream Buffer Strips

To illustrate how the operational framework might be applied, consider the Tongass National Forest policy requiring buffer strips to be left on larger, non-fish bearing headwater streams (USDA Forest Service 1997). The intent of these buffer strips is to help control the flow of debris from adjacent hillslopes into headwater streams, and on down into fish-bearing reaches below (Everest et al. 1995). The requirement for headwater buffers calls for narrower strips to be left than on lower gradient, fish bearing streams. Only incised headwater streams receive this protection, and only within the v-notch, up to the first slope break.

This management policy, new in TLMP, was recommended by a team of watershed scientists as a result of a Congressionally-sponsored review of fish habitat protection measures on the Tongass (Everest et al. 1995), where natural runs of all native salmon species still thrive and where their harvest is still the backbone of the region's economy. The scientists felt that headwater streams play a critical role in determining the regime of sediment delivery to fish habitat below, and that headwater buffer strips are needed to ensure that the sediment delivery regime is not disrupted by timber harvest. For southeastern Alaska at least, this recommendation derived from expert judgments,

not, for the most part, from scientific studies that had clearly demonstrated this relationship.

Tongass managers find this policy especially costly. Stream density in the rainforests of southeastern Alaska is so high that it is virtually impossible to lay out a timber harvest unit without including at least one, and often more, streams that fall under the headwater buffer strip requirement. Planning a timber sale becomes more complicated because every individual rill must be mapped precisely. For each stream segment, a determination of whether a buffer strip is required must be made, based on characteristics of channel morphology, which themselves must be measured in detail. Each buffer strip must be mapped and flagged. The area of buffer strips must be subtracted from the total area of the unit, using GIS software, to arrive at the amount of timber to be offered for sale. The logging system to be used must be designed so that trees can be extracted from the harvested strips between protected streams without disturbing any stream buffers. During harvest, the timber sale administrator must work closely with the logging contractor to ensure the buffer strip requirements are understood and respected, and to solve logistical problems that inevitably come up as the logging equipment is maneuvered around the protected strips. Clearly the headwater buffer strip requirement fits the definition of a management policy ripe for effectiveness monitoring, since it is a cornerstone of the freshwater habitat conservation strategy but costly to implement, and many of the scientific assumptions underlying this policy have yet to be tested for the climatic regime and physical topography of southeastern Alaska.

To properly evaluate this policy, all four components of the monitoring framework are needed. It goes almost without saying that implementation monitoring

will be critical, not just because other monitoring cannot be carried out without assurance that the policy is being applied as intended, but because this practice calls for timber sale layout crews to develop new skills and exercise judgment in new ways – their responsibilities have been expanded. Indeed, early implementation monitoring of this policy exposed inconsistencies in the way it was being applied and required clarifications such as a more detailed description of the criteria for determining which headwater streams the buffer strip requirement applied to. Other results included such simple changes as standardizing the colors of flagging that would be used to mark different types of headwater streams, and clarifying whether stream incision depth should be measured vertically or along the slope perpendicular to the stream channel. It should be noted that while those sorts of immediate payoffs from implementation monitoring tend to drop off over the life of a management practice, periodic turnovers in field personnel make it important that implementation monitoring continue indefinitely to quickly catch any problems that result from replacing veteran practitioners with ones new to the game.

The second component of the monitoring framework is periodic inventories. A current baseline map of all stream channels was alluded to in the previous section. From this, the set of all stream reaches that are candidates for headwater buffer strip protection can be determined. This set can be periodically intersected with a current map of existing timber harvest to inventory headwater streams that are unharvested, streams that were harvested without buffer strip protection, and streams harvested with buffer strips left in place. This inventory has at least two functions: (1) cumulative effects assessment; and (2) identification of candidate sites for testing hypotheses about the function of buffer strips on headwater streams. Other inventories that may be relevant include the locations

of mass wasting events and of buffer strip blowdown events. Such inventories can be used in a variety of ways to support the implementation of the headwater buffer strip policy and the remaining two components of the monitoring framework.

The third component of the monitoring framework is tests of the effectiveness of specific management practices. By this, we mean the measurement of one or more quantitative variables that can be tested against some value or range deemed to indicate proper ecosystem function, or the lack thereof. What we do not mean is what typically constitutes a monitoring program: an unfocused effort to measure a few randomly chosen quantities at an unspecified level of resolution with unknown error, and an expectation that any problems will somehow make themselves apparent by exhibiting a strong signal that stands out from the background noise. It would be rare for a scientific researcher to receive funding for such an ill-considered fishing expedition, and it's no surprise that natural resource managers are reluctant to dedicate fiscal resources to monitoring programs that fit this description.

The stated purpose of headwater buffer strip protection in TLMP is to maintain the pre-harvest sediment delivery regime to fish-bearing reaches downstream. Since the goal is not a particular rate of sediment delivery but a pattern over time, the pre-harvest pattern of sediment delivery must be known in order to select criteria against which to evaluate effectiveness. The interval over which sediment delivery will be monitored must be specified, along with the resolution and known error of delivery rate measurements. A sampling design must be developed that controls for background variation and provides sufficient power to detect a change in sediment delivery regime. It is no small matter to specify what sort of regime change would be an indication of altered

ecosystem function, but it should be clear that a monitoring program cannot be designed to produce scientifically credible conclusions if these steps, which are second nature for most scientific researchers, are not first followed. It is difficult to understand how credible environmental monitoring can be proposed that does not adhere to the same principles of study design as other scientific research, but it is not hard to see why monitoring programs have developed a poor reputation as a result of failing to adhere to those principles.

Finally, the fourth monitoring component, the one likely to be of greatest interest to researchers and of greatest concern to managers, is testing the key assumptions that underlie a management policy. For the headwater buffer strip policy, those assumptions would include: (1) that sediment delivery regime is an important determinant of fish habitat quality downstream; (2) that sediment delivery regime is largely controlled upstream of fish-bearing reaches; and (3) that riparian vegetation along high-gradient stream reaches is an important regulating mechanism for sediment delivery. To address these questions, a series of rigorous scientific studies would be needed, and managers must work closely with researchers to design study objectives that are pertinent yet achievable with the resources available (Walters 1997). An important point is that the operational framework we propose considers these sorts of studies, along with the other three components discussed above, to all be part of the monitoring program. The dictionary definition of "monitoring" refers to something that is systematically tracked or measured on an ongoing basis (American Heritage Dictionaries 2000), and many people assume that "monitoring" can only describe activities that involve repeat sampling over a long or indefinite time period. We argue that in the natural resource management

context, the word "monitoring" has come to be shorthand for "monitoring and evaluation," and that it is actually the second of those two words that best defines the activity. This use of the term makes it clear that rigorous scientific tests of underlying assumptions fit squarely within a monitoring program, even, and especially, if they are completed in a finite time.

ROLES OF THE PLAYERS

If scientists are to be funded by resource management agencies to do this sort of research, they must take responsibility for ensuring that policy makers understand the implications of their results for existing management policies, and thereby contribute to closing the adaptive management loop. For example, a number of academic studies of genetic population structure of various small mammals have been conducted, with agency support, during the last decade (*e.g.* Cook et al. 2001). Taken together, they suggest that not only is there a high degree of endemism in the Tongass, but that most endemics are restricted to just a few of the islands and even within subspecies there is considerable island-based population structuring. The present Tongass conservation strategy does not consider that individual populations should be managed separately. All members of a species are considered to be members of a single population that spans the range inhabited by the species in southeastern Alaska. Cook et al (2001, p. 224) include a brief sentence at the end of their manuscript suggesting that this perspective needs reconsideration: "At a minimum, distinctive regions should be managed independently given that they support reciprocally monophyletic lineages and thus, distinctive regional biotas." For managers to take notice, understand the implications, and determine specific

policy modifications to address this concern, a single sentence in a journal not generally read by policy makers is not sufficient. We believe that resource management agencies should be more generous in providing support for basic research conducted in the ecosystems that they manage, but that researchers must compensate this generosity at the conclusion of studies by collaborating with managers to achieve a mutual understanding of how their results alter the assumptions that existing policies are built on.

The most effective monitoring program for a large-scale conservation strategy will include active participation of both agency biologists and research biologists, as well as substantial interaction between them. Agency biologists and their coworkers must set the objectives of the monitoring program and define the level of effort that will be committed to it. They will be responsible for much of the data collection, and for recruiting and training the crews that collect it. But agency biologists do not always have the training to develop efficient, objective sampling designs, nor to select or apply the most appropriate statistical methods for data analysis. Research biologists can help to improve the quality and efficiency of agency monitoring programs by serving as consultants and reviewers, just as they did, in the case of the Tongass, during the original development of the TLMP conservation strategy (Mills et al. 1998).

On the Tongass, implementation monitoring is primarily the province of agency biologists. Verifying that planned actions have been carried out and guidelines followed is a relatively straightforward task. There is some challenge in choosing an efficient and objective sampling scheme for implementation monitoring, and here research biologists may be able to assist. A second challenge is in deciding which aspects of policy implementation merit monitoring. Here, it would be best to examine the objectives of the

remainder of the monitoring program. It will be difficult indeed to evaluate the effectiveness of a policy such as the Tongass conservation strategy if it is unknown whether the strategy has in fact been implemented. Where the effectiveness of the strategy is believed to rest on key aspects of the policy, these aspects should be included in the program of implementation monitoring. Here, a mixed team of researchers and agency biologists will be most likely to ensure that aspects of the policy that are most important for conservation are not inadvertently omitted from the implementation monitoring program, nor is too much effort expended on monitoring the implementation of uncontroversial components of the policy (uncontroversial meaning here that correct implementation is sufficiently likely as to not need verification).

Defining the objectives of a monitoring program is clearly the province of resource managers, since the monitoring program exists to serve their information needs. Only the agency can decide, as well, what level of effort to invest in a monitoring program (unless that is decided at a higher level, in Congress or in the courts). But vague objectives will doom many scientific endeavors. Choosing and articulating well-focused objectives is a skill that researchers practice regularly. As reviewers, researchers can help agency managers and biologists ensure that the objectives defined for a monitoring program are focused and clearly stated. Tight collaboration at this stage is critical. Agency representatives must identify in some detail the aspects of management policy about which information is most needed or researchers may focus on questions they find more academically interesting.

Researchers can also help agency personnel determine the most effective methods for addressing those objectives and realistically chart the resources required to meet

monitoring goals. In general, agency biologists attend far fewer scientific meetings and seminars and do not have the breadth of experience that researchers can offer when selecting methods and study designs. Researchers tend to be more familiar with the application of cutting edge technologies to scientific investigation, and with a broad pallet of techniques for data analysis and particularly for recognizing and dealing with unruly data. In turn, agency collaborators typically take responsibility for the bulk of actual monitoring data collection. Researchers are thus freed up to spend more time thinking, almost an unspeakable luxury but one that can have profound benefits for the monitoring program overall.

An important role for researchers in a monitoring program is in testing key assumptions that underlie the policy being evaluated. Just as some of the science that was used to develop the strategy was the product of academic researchers, so will new basic science be central to policy revisions. It is to be expected that from time to time basic scientific investigations will uncover flaws in the strategy that derived from the acceptance of inappropriate assumptions. These deeply buried flaws can be resistant to discovery by those who are testing the strategy directly. Such tests normally attempt to control for sources of unexpected variation and because of this can become almost self-fulfilling prophesies at times. For instance, a monitoring study of the effectiveness of riparian buffer strips may collect data only in the buffer strip itself and find that, say, amphibian densities appear to be healthy there, but fail to notice that the buffer strip is actually acting as a sink for amphibians immigrating from unharvested forest upstream.

The roles we have proposed for agency and research biologists in developing and implementing a large monitoring program are notably different from what typically

happens at present. In particular, we believe that more use should be made of researchers as reviewers and consultants, and at more stages in the development and execution of the monitoring program. We believe that poorly focused objectives and limited scientific rigor doom many monitoring programs. Skills to address those problems are regularly taught by research scientists associated with graduate programs, but researchers may have difficulty seeing the merit of adding to their workload by adopting a second cohort to mentor. We argue that there are substantial benefits to *both* sides. Among other things, researchers who regularly advise agency biologists should be among the best candidates for receiving funding to conduct research associated with monitoring programs. Not only will they be familiar with the questions the agency is wrestling with, and the state of current knowledge, but they will be at an advantage when it comes to planning and arranging for logistical support. In the Tongass, arranging for logistical support is one of the biggest obstacles to conducting field research, so much so that academic researchers rarely undertake any but the most trivial studies if they are not affiliated with an agency that can provide local support.

Another benefit of contributing to the scientific rigor of the collection of monitoring data is that such data may later be mined by researchers for other purposes. Few researchers have the means to collect data on such a large scale as many resource management agencies do routinely. Resource management agencies have larger staffs than most ecological research labs, and they have the infrastructure to support the logistics of large-scale data collection. Field-collected datasets are never without their deficiencies, but the early participation of researchers in the design of monitoring protocols can reduce deficiencies and increase the utility of the resulting datasets. In my

own research, I have been able to greatly increase the extent and variety of data that could be searched for patterns and used for hypothesis testing by adding to my data a number of datasets collected by agency biologists during the preceding 50 years (Hastings 2005). Unlike researchers whose careers depend on the primacy of their discoveries, I have found publicly-funded resource management agencies to be more than willing to share their data unless it is of a sensitive nature (*e.g.* nesting sites of individuals of an endangered species).

CONCLUSIONS

The central challenges of evaluating the effectiveness of a large, distributed reserve system are a result of the size and complexity of the ecosystems, the fact that the "treatment" being evaluated is not static, and the diverse backgrounds and approaches of the people involved in the evaluation. The challenges posed by large size and complexity can be somewhat tamed by developing good inventories and spatially explicit distribution maps for all taxa, and for significant habitat features and anthropogenic developments. The moving target constraint requires that the monitoring program not be entirely fixed in stone and temporally invariant for the foreseeable future, but rather include a selection of continuously changing smaller studies that are integrated by an operational framework and periodic syntheses of results and implications. The diversity of players is a strength, but only if all participate according to what they can best contribute. Researchers, in particular, must make the effort to overcome the attitude that evaluating the effectiveness of conservation strategies, aka "monitoring", is uninteresting and beneath them. The logistical resources of large management agencies make large-scale data collection

possible and offer the researcher the luxury of spending the lion's share of her or his time on analysis and interpretation.

Far more work has gone into designing and implementing ambitious conservation strategies than into evaluating them at this point. We believe that the best strategy for evaluating the effectiveness of large, distributed reserve networks remains an open question. We suggest that a symposium or workshop should be convened around this topic soon, as the pressure to demonstrate the value of costly conservation measures such as reserve set-asides is sure to increase in concert with increasing human population size. As a first step, the goals for different reserve networks should be articulated, perhaps with the aim of developing a classification of reserve network types. Such as classification could support a conceptual framework for reserve system evaluation that is generalizable to different continents, different political settings, and both terrestrial and aquatic reserves. We can envision the emergence of specialized subdisciplines such as spatial statistics for reserve-corridor configurations, and the extension of ecoinformatics into the arena of managing large volumes of spatially and temporally repeated measurements. The core question of reserve network evaluation offers no shortage of intellectual challenge, and the potential reward of seeing ones work translated into highly visible, measurable (and measured!) conservation gains.

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APPENDIX 1. Southeast Alaskan sites where uplifted glaciomarine sendiments have been reported. A few sites with other physical evidence of uplift are included

ID	Elevation (ft ASL)	Date (BP)	Material	General Location	Reference ID	Source	Comments
AD1	695	?	Shell	Admiralty	S. Fk. Bear Creek, Mansfield Peninsula	Miller 1973b, cited by Mann 1986 p. 255	Glaciers retreated before this deposit was laid down
AD2	105	9200+/-80	Wood	Admiralty	GREENSCREEK1 (Kennecott-Greens Creek Mine)	Baichtal 2001	Sample recovered during subsurface drilling...depth of 10' - 10'8". Sample from peat sitting atop shell bearing sand and silt deposit.
AD3	105	12300+/-80	Shell	Admiralty	GREENSCREEK2 (Kennecott-Greens Creek Mine)	Baichtal 2001	Sample recovered during subsurface drilling...depth of 10' - 10'8". Sample from shell bearing sand and silt deposit immediately beneath GREENSCREEK1.
CH1	230	12130+/-110	Shell	Chichagof	SI-2082 ("NE Chichagof")	Mann 1986 p.255; Mobley 1988 Table 1, from Mann 1986	

ID	Elevation (ft ASL)	Date (BP)	Material	General Location	Reference ID	Source	Comments
CH2	262	?	Strandflat topography	Chichagof	"Chichagof Mining District", W Chichagof	Reed and Coats 1941 p. 75, cited by Mann 1986 p.252 & 254	
CP1	33-49	?	Shell	Chilkat Peninsula	Ground Hog Bay	Mobley 1988 p. 262, from Ackerman et al 1979	
CP2	39-49	13350+/-100	Shell	Chilkat Peninsula	SI-2114 (Point Couverden)	Mobley 1988 Table 1, from Mann 1986 p 257, from Ackerman et al 1979	Mobley 1988, citing Mann 1986, places this and CP4 "farther north at Glacier Bay", relative to Ground Hog Bay at Point Couverden. Mann 1986 p 257, however, says "Point Couverden", citing Ackerman et al 1979 as his source,and also says this is SI-2082, which conflicts with Mobley 1988.
CP3	39-49	9220+/-80	Charcoal	Chilkat Peninsula	SI-2115 (Point Couverden)	Mobley 1988 Table 1, from Mann 1986 p 257, from Ackerman et al 1979	Dates the time of emergence of CP2 (not later than CP3)

ID	Elevation (ft ASL)	Date (BP)	Material	General Location	Reference ID	Source	Comments
CP4	16-21	Older than 9000	Terrace	Chilkat Peninsula	Point Couverden	Mobley 1988 Table 1, from Mann 1986 p 257, from Ackerman et al 1979	Essentially the same location as CP2/CP3
CP5	11	3000-3500	Terrace	Chilkat Peninsula	Point Couverden	Mobley 1988 Table 1, from Mann 1986 p 257, from Ackerman et al 1979	Essentially the same location as CP2/CP3
DI1	533	13450+/-190	Shell	Douglas	FISH CREEK	Baichtal 1999	Baichtal (2003 unpublished data) updates elev from 151m to 164m
DI2	~45	9800+/-300	Shell	Douglas	W2392 (mouth of Cove Creek)	Miller 1972 p.96	Deposits in Juneau area laid down under no more than 30 m of water (Miller 1972 p. 93)
DI3	106	9150+/-800	Shell	Douglas	W2395 (gravel pit at Eagle Creek)	Miller 1972 p. 71, Miller 1973b p. 314	Glaciomarine shell deposit above sand and gravel in older delta deposit
DI4	80	10760+/-500	Shell	Douglas	W2394 (gravel pit at Eagle Creek)	Miller 1973b p. 314	Glaciomarine shell deposit beneath sand and gravel in older delta deposit

ID	Elevation (ft ASL)	Date (BP)	Material	General Location	Reference ID	Source	Comments
DI5	55	9700+/-800	Shell	Douglas	W2393 (Kowee Creek)	Miller 1972 p.98; Mobley 1988 Table 1, from Swanston 1984	Youngest date on glaciomarine deposit near Juneau
DI6	200	?	Beach deposits	Douglas		Buddington 1927 p. 51, citing Dall	No detailed location or citation available
DI7	425	?	Shell	Douglas	On trail above Treadwell glory hole	Twenhofel 1952 p. 528	Twenhofel 1952 p. 528 has other lower Douglas glaciomarine sites
DI8	500	?	Shell	Douglas	On Treadwell Ditch between Paris and Boullion Creeks	Twenhofel 1952 p. 528	Twenhofel 1952 p. 528 has other lower Douglas glaciomarine sites
ET1	122	12540 +/- 180	Shell	Etolin	ETOLIN1 (Logjam Creek)	Baichtal 2000	Shell from the bed of Logjam Creek, 4.5 miles from mouth.
GR1	80	?	Shell	Gravina	Southern end of Gravina, 0.5 mi NW of the head of Dall Bay	Berg 1973 p. 35, Lemke 1975 p.8, Buddington 1927 p. 51, all from Chapin 1918	Lemke and Yehle 1972 p.13 give this height as 85 feet.

ID	Elevation (ft ASL)	Date (BP)	Material	General Location	Reference ID	Source	Comments
GR2	7	13720 +/- 90	Shell	Gravina	KET59301 (Seal Cove, Gravina Island)	Baichtal, 2003 unpublished data	
HA01	25	?	Clay and silt	Haines	8-144	Lemke and Yehle 1972, Table 2	
HA02	30	?	Shell	Haines	7-324	Lemke and Yehle 1972, Table 2	
HA03	25	?	Clay and silt	Haines	8-141	Lemke and Yehle 1972, Table 2	
HA04	14	?	Shell	Haines	8-109	Lemke and Yehle 1972, Table 2	
HA05	15	?	Shell	Haines	5-224	Lemke and Yehle 1972, Table 2	
HA06	12	?	Shell	Haines	8-108	Lemke and Yehle 1972, Table 2	
HA07	45	?	Clay and silt	Haines	8-107	Lemke and Yehle 1972, Table 2	
HA08	50	?	Shell	Haines	8-142	Lemke and Yehle 1972, Table 2	

ID	Elevation (ft ASL)	Date (BP)	Material	General Location	Reference ID	Source	Comments
HA09	50	?	Shell	Haines	5-223	Lemke and Yehle 1972, Table 2	
HA10	50	11020+/-400	Shell	Haines	W-2294	Mobley 1988 Table 1, from Lemke and Yehle 1972 p.13	
HE1	20	6820 +/- 60	Shell	Heceta	CHUCK1 (Chuck Lake)	Baichtal 2000	Shell (*Saxidomus giganteus*) eroding from scour pool in the creek bed.
HE2	7	9410+/-130	Shell	Heceta	WSU-3239 (Rice Creek)	Mobley 1988 Table 2, from Ackerman et al 1985	
HE3	23	9450+/-70	Shell	Heceta	CHUCK2 (Chuck Lake)	Baichtal 2001	Chuck Lake Inlet Stream
IS1	33-49	13420+/-130	Shell	Icy Strait	SI-2082	Mobley 1988 Table 1, from Ackerman et al 1979	Location very uncertain
IS2	33-49	11630+/145	Shell	Icy Strait	SI-2113	Mobley table 1, from Ackerman et al 1979	Location very uncertain

ID	Elevation (ft ASL)	Date (BP)	Material	General Location	Reference ID	Source	Comments
JU01	627	13060+/-40	Shell	Juneau	SPAULDING 2	Baichtal 1999	
JU02	80	10640+/-300	Shell	Juneau	W1827 (Jct of Fritz Cove Rd and Glacer Hwy)	Miller 1972 p.93	Miller 1973a p. C4 says "opposite parking lot at Auke Lake."
JU03	~400	11920+/-1000	Shell	Juneau	W2396 (Salmon Creek valley)	Miller 1972 p.93	Miller 1973a p. C4 says "where trail to Salmon Creek Reservoir crosses scarp."
JU04	750	12900?	Shell	Juneau	Upper Montana Creek	Miller 1972 p.94	Date is from Mann 1986 p.252
JU05	98	10630+/-500	Shell	Juneau	W2363 (in drainage ditch embankment of college parking lot, Auke Lake)	Miller 1972 p.98, Miller 1973a C5	
JU06	138	10240+/-300	Shell	Juneau	W-1826 (roadcut in interfluve between Auke Lake and Montana Creek valley)	Miller 1973a C5	
JU07	633	?	Shell	Juneau	"Juneau"	Yehle 1978 p.16, from A.C.Spencer (Buddington and Chapin 1929 p. 278; Smith 1965 p. 27)	

ID	Elevation (ft ASL)	Date (BP)	Material	General Location	Reference ID	Source	Comments
JU08	630	?	Shell	Juneau	"Juneau"	Yehle 1978 p.16, from Miller 1975	
JU09	102	12730+/-500	Shell	Juneau	W-1830 (Gravel pit near Auke Bay ferry terminal)	Miller 1972 p. 70, Miller 1973a C6	Glaciomarine shell deposit above sand and gravel in older delta deposit
JU10	60	12880+/-500	Shell	Juneau	W-1831 (Gravel pit near Auke Bay ferry terminal)	Miller 1972 p. 70, Miller 1973a C6	Glaciomarine shell deposit beneath sand and gravel in older delta deposit
JU11	190	10880+/-340	Shell	Juneau	W-1829 (Near the mouth of Gold Creek)	Miller 1972 p. 70, Miller 1973a C6	
JU12	100	?	Fossils in marine gravels	Juneau	Summit of the divide through which the Amalga tramway passes after leaving the flats of Eagle River	Budington 1927, citing Knopf 1912. Also Twenhofel 1952 p. 530.	Knopf also found marine gravels along Lemon Creek and Eagle River
JU13	425	?	Shell	Juneau	NW bank of McGinnis Creek 1 mile upstream from mouth	Twenhofel 1952 p. 528	Twenhofel 1952 p. 528 has other lower Juneau glaciomarine sites
JU14	?	12300+/-350	Shell	Juneau	W-1839 (Gravel pit near Auke Bay ferry terminal)	Miller 1973a C14, from Marsters et al 1969	Same deposit and area as JU09 (W-1830) and JU10 (W-1831)
KE01	40	12640+/-90	Shell	Ketchikan	SCHMOLK 1	Baichtal 1999	

ID	Elevation (ft ASL)	Date (BP)	Material	General Location	Reference ID	Source	Comments
KE02	70	12710+/-70	Shell	Ketchikan	SCHMOLK 2	Baichtal 1999	
KE03	69	12800+/-240	Shell	Ketchikan	HILL 1	Baichtal 1999	
KE04	79	13440+/-370	Shell	Ketchikan	HILL 2	Baichtal 1999	
KE05	101	13050+/-50	Sediment	Ketchikan	LIGHTHOUSE	Baichtal 1999	Two more dates available from layers on top of this sample. Pine was growing here at 11660 +/- 100 BP.
KE06	176	13430+/-50	Sediment	Ketchikan	VALENTINE	Baichtal 1999	
KE07	85	?	Shell	Ketchikan	In the city of Ketchikan	Lemke 1975 p.8	Lemke and Yehle 1972 p.13 give this height as 83 feet.
KE08	59-98	?	Shell	Ketchikan	Saxman, Mountain Pt	Lemke 1975 p.8	
KE09	300	?	Shell	Ketchikan	"NE Revilla"	Lemke 1975 p.8, from Tobin 1969	Elevation "was an estimate only and may be in considerable error."
KE10	197	?	Marine terraces	Ketchikan	"Near Ketchikan"	Mann 1986 p.254, from Berg 1973; also Mobley 1988 p.262, from Berg 1973	Perhaps the marine terrace with wave-cut cliff in Blank Inlet, Gravina?

ID	Elevation (ft ASL)	Date (BP)	Material	General Location	Reference ID	Source	Comments
KE11	33	7230+/-115	Shell	Ketchikan	SI-906 (Orton Ranch)	Mobley 1988 Table 1, from Stuckenrath 1971	
KE12	33	8420+/-120	Shell	Ketchikan	SI-905 (Orton Ranch)	Mobley 1988 Table 1, from Stuckenrath 1971	
KU1	98	13270 +/- 50	Shell	Kupreanof	KUPREANOF1 (Todahl Creek)	Baichtal 2000	Shell from glaciomarine sediments in stream bank.
KU2	98	13230 +/- 40	Shell	Kupreanof	KUPREANOF2 (Todahl Creek)	Baichtal 2000	Shell from glaciomarine sediments in road cut.
KU3	135	12440 +/- 120	Shell	Kupreanof	KUPREANOF3 (E of Todahl Creek)	Baichtal 2000	Shell from glaciomarine sediments in road cut.
MA1	492	?	Glacial marine clays	Mainland	Mainland east of POW	Mann 1986 p.254, from McConnell 1913	Probably at head of Portland Canal
MA2	13-59	?	Shell-bearing sand and/or pebble gravel	Mainland	"NE Frederick Sound and farther north and northwest"	Yehle 1978 p.15	Relict shore and delta deposits.

ID	Elevation (ft ASL)	Date (BP)	Material	General Location	Reference ID	Source	Comments
MA3	175-200	?	Fossils in clay overlain by coarse gravels	Mainland	About 0.5 mi up Goat Creek, trib of the Stikine River about 5 mi above the international boundary	Budington 1927, also Twenhofel 1952 p. 526.	
MA4	?	?	Shell	Mainland	Moraine of Great Glacier	Twenhofel 1952 p. 526, citing Budington and Chapin 1929	"It apears that the locality is less than 100 feet above sea level."
MA5	178	13070 +/- 80	Shell	POW	SNIPEPOINT1 (Bell Island)	Baichtal 2000	Shell from glaciomarine sediments in stream channel. Volcanic glass in sediments.
MI1	~140	3790+/-70	Wood	Mitkof	PETERSBURG 1	Baichtal 1999	From base of peat layer atop glaciomarine sediments in cutbank.
MI2	205 Ives	12400+/- 800	Shell	Mitkof	"E" (see Yehle 1978 fig 2 map). Also W1734 (Ives: from pit 2 mi SE of Petersburg, 56-47-48N 132-54-40W).	Yehle 1978 p.13; Ives 1967 p. 524.	Lemke 1974 p.15 gives the elevation as 212'. Mobley 1988 says "species analysis did not necessarily indicate a shore environment of deposition."

ID	Elevation (ft ASL)	Date (BP)	Material	General Location	Reference ID	Source	Comments
MI3	26	9970+/-300	Shell	Mitkof	M-2541 ("D", Blaquiere Pt)	Yehle 1978 pp.12 & 14. Also W-1738 in Ives 1967 and in Mobley 1988 Table 1, from Yehle 1978.	
MI4	52	?	Shell	Mitkof	M-2543 ("A", W of Banana Pt)	Yehle 1978 p.12	
MI5	46	?	Shell	Mitkof	M-2542 ("C", SW of Blaquiere Pt)	Yehle 1978 p.12	
MI7	125	12170+/-400	Shell	Mitkof	M-3944 ("B", Banana Pt))	Yehle 1978 pp.12 & 14	Mobley 1988 Table 1 calls this W-2327.
MI8	244	?	Shell-bearing sand and/or pebble gravel	Mitkof	Twin Creek	Yehle 1978 p.15	Relict delta. Lower edge is at 60 m.

ID	Elevation (ft ASL)	Date (BP)	Material	General Location	Reference ID	Source	Comments
PC1	450	?	Marine blue clay	Portland Canal	Kitsault River and its northeast fork	Twenhofel 1952 p. 524 and Lemke and Yehle 1972 p.13, both from Hansen 1923 p. 40	
PC2	343-348	?	Marine clay with shells	Portland Canal	Bear River above its junction with Bitter Creek	Twenhofel 1952 p. 524 and Lemke and Yehle 1972 p.13, both from McConnell 1913 p. 22	"Similar clays without shells…occur a mile farther up the valley up to an elevation of 485 feet."
PC3	450	?	Clays	Portland Canal	Salmon River, near Elevenmile, Alaska, on the road between Hyder and the Premier Mine	Twenhofel 1952 p. 524, citing Schofield and Hanson 1922 p. 27-28. Also Budington 1927 p. 51.	"…they considered thse sediments to be elevated delta deposits formed by the Salmon River when sea level was 450 feet higher."
PW01	10	9400+/-70	Shell	POW	THORNE 1	Baichtal 1999	
PW02	10	8770+/-70	Shell	POW	THORNE 4	Baichtal 1999	

ID	Elevation (ft ASL)	Date (BP)	Material	General Location	Reference ID	Source	Comments
PW03	10	5170 +/- 70	Shell	POW	REDCREEK1 (Red Bay Lake Creek)	Baichtal 2000	Shell (*Saxidomus giganteus*) eroding from scour pool in the creek bed.
PW04	13	?	Charcoal	POW	REDCREEKM1 (Red Bay Lake Creek)	Baichtal 2000	Charcoal from possible hearth excavated into compacted glacial till.
PW05	13	?	Charcoal	POW	REDCREEKM2 (Red Bay Lake Creek)	Baichtal 2000	Charcoal from midden in contact with compacted glacial till.
PW06	13	?	Charcoal	POW	REDCREEKM3 (Red Bay Lake Creek)	Baichtal 2000	Charcoal from midden in contact with compacted glacial till.
PW07	13	?	Shell	POW	REDCREEKM4 (Red Bay Lake Creek)	Baichtal 2000	Shell (*Protothaca* sp.) from midden in contact with compacted glacial till.
PW08	-2	1790 +/- 60	Shell	POW	REDLAKE1 (Red Bay Lake)	Baichtal 2000	Shell (*Protothaca sp.*) from a sandy silt layer 12-15 feet below the surace of Red Bay Lake. *Saxidomus giganteus* also found at this site.
PW09	30	9450 +/- 80	Shell	POW	NARROWPOINT1 (14 km N of Thorne Bay)	Baichtal 2000	Shell (contents of worm/clam tubes) from glaciomarine sediments in road cut just before MP. 27, Forest Road 30, E. POW
PW10	39	8990 +/- 50	Shell	POW	OYNWB1 (Protection Head)	Baichtal 2000	Shell from excavation. Raised beach in west end of karst channel.

ID	Elevation (ft ASL)	Date (BP)	Material	General Location	Reference ID	Source	Comments
PW12	66	37370 +/- 1520	Shell	POW	LAVA1 (Lava Creek, by Salmon Bay)	Baichtal 2000	Shell from glaciomarine sediments exposed in slide on stream bank. Lava Creek upstream of Forest Road 30 bridge.
PW13	200	?	Marine till	POW	"Craig C-2"	Mann 1986 p.252 & 254, from Sainsbury 1961	Sainsbury 1961 p. 351 says only that a marine tilll "without shells was found at an altitude of almost 200 feet in the valley of Maybeso Creek, just west of the south end of the mapped area."
PW14	50	?	Barnacles and small pelecypods	POW	Coal Bay	Mobley 1988 p.262, from Sainsbury 1961 p. 330.	Sainsbury 1961 p. 351 says "in the stream at Little Coal Bay." Also "similar till is exposed at an altitude of 380 feet on the hill to the southeast" (p. 331).
PW15	3	500+/-45	Shell	POW	SI-914 (Karta Bay)	Mobley 1988 Table 2	
PW16	6	7620+/-120	Shell	POW	BETA-20555 (Red Bay)	Mobley 1988 Table 2	
PW17	8	7630+/-80	Shell	POW	BETA-9488 (Yatuk Creek)	Mobley 1988 Table 2	
PW18	10-Jul	7970+/-90	Shell	POW	BETA-20557 (Exchange Cove)	Mobley 1988 Table 2	

ID	Elevation (ft ASL)	Date (BP)	Material	General Location	Reference ID	Source	Comments
PW19	0-3	8310+/-80	Shell	POW	BETA-20554 (Big Creek)	Mobley 1988 Table 2	
PW20	10	8440+/-100	Shell	POW	BETA-9487 (ULMB Site)	Mobley 1988 Table 2	
PW21	30	9510+/-280	Shell	POW	I-1621 (Harris River)	Mobley 1988 Table 2; Mann 1986 p.254, from Swanston 1969 p. 31	
PW22	4	9510+/-90	Shell	POW	BETA-20556 (Red Bay)	Mobley 1988 Table 2	
PW23	?	?	Shell	POW	Lower valley of Maybeso Creek	Sainsbury 1961 p. 331	Differs from PW13 which doesn't have shells present
PW24	?	?	Shell	POW	Above high-tide level at the mouth of the small stream that flows northeastward into Clarence Strait from Salamander Lake	Sainsbury 1961 p. 351	

ID	Elevation (ft ASL)	Date (BP)	Material	General Location	Reference ID	Source	Comments
PW25	35	8780+/-70	Shell	POW	EFSC1s (E Fk Staney Ck)	Baichtal 2001	
PW26	36	7670+/-80	Shell	POW	EFSC2s (E Fk Staney Ck)	Baichtal 2001	
PW27	36	7020+/-40	Wood	POW	EFSC2w (E Fk Staney Ck)	Baichtal 2001	Sample is a water worn piece of root or knot from within shell layer
PW28	38	7910+/-70	Shell	POW	EFSC3s (E Fk Staney Ck)	Baichtal 2001	
PW29	38	7380+/-60	Wood	POW	EFSC3w (E Fk Staney Ck)	Baichtal 2001	Sample is from a layer of marine silt immediately above the shell layer
PW30	41	9210+/-60	Shell	POW	EFSC4s (E Fk Staney Ck)	Baichtal 2001	
PW31	36	9340+/-70	Shell	POW	BSL1 (Big Salt Lake)	Baichtal 2001	Big Salt Lake, SE Shore
PW32	40	9370+/-80	Shell	POW	KLAWOCK1 (Klawock Lake)	Baichtal 2001	Discovered in less than 1 foot of water along the lake's shore. Samples not in situ.
SI1	35	?	Elevated shore deposits and deltas	Sitka	"Swan Lake to Indian River"	Yehle 1974 p.25	Other possible elevations from Yehle 1974 p.14: 50' (landforms); 65' (whale vertebra in a sand deposit); 250' (widespread abrupt change in steepness of slope).
SI2	200	?	Marine terraces	Sitka	"Sitka area"	Arndt 1987 from Swanston 1984	Tentatively correlated with the upper marine limit along the inner coast to the east of Baranof Island

ID	Elevation (ft ASL)	Date (BP)	Material	General Location	Reference ID	Source	Comments
TU1	~20	9210 +/- 70	Shell	Tuxekan	TUXEKAN1 (S Tuxekan)	Baichtal 2000	Shell from glaciomarine sediments exposed in stream bank.
WR1	~100	12010 +/- 280	Shell	Wrangell	WRANGELL1 (11 mi S of Wrangell)	Baichtal 2000	Shell from construction site.
WR2	At least 150	?		Wrangell	"Wrangell area"	Lemke 1974 p.19	
WR3	52	?		Wrangell	M-5757, roadcut at the SE edge of the Wrangell airport apron	Lemke 1974 p.20	Elevation is given as 60 ft above MLLW or 52 ft above MSL.
WR4	72	?	Shell	Wrangell	M-5756, halfway down the runway on the SW embankment at the Wrangell airport	Lemke 1974 p.22	
WR5	180	?	Sand and gravel	Wrangell	"Quarry 1 mi N of Wrangell"	Lemke 1974 p.25	
WR6	70	9700+/-350	Shell	Wrangell	W2326 -- Wrangell vicinity	Lemke 1974 p.26	Mobley table 1 says this elevation is 21m ASL.
WR7	60-120	?	Shell	Wrangell	"Within Wrangell corporate limits"	Lemke 1974 p.26	
WR8	?	?	Shell	Wrangell	In the town of Wrangell in the excavation for the old cable office	Twenhofel 1952 p. 526, citing Budington and Chapin 1929	"It apears that the locality is less than 100 feet above sea level."

APPENDIX 2. Allele frequencies at eight microsatellite loci in coastal cutthroat trout from isolated headwater streams in southeastern Alaska.

	OMY77															
	*106	*108	*114	*118	*120	*122	*124	*126	*128	*130	*132	*134	*136	*138	*140	*142
DNA	---	---	---	0.650	---	---	---	---	---	0.133	---	---	0.200	0.017	---	---
DNB	---	---	0.045	0.152	0.121	---	---	0.015	---	0.227	0.106	---	0.303	0.030	---	---
DSA	0.481	---	---	---	0.111	---	---	0.130	---	---	0.259	---	0.019	---	---	---
DSB	0.214	0.024	---	---	0.143	---	---	0.071	---	0.048	0.190	0.048	0.190	0.071	---	---
JEA	---	---	---	---	0.117	---	---	---	---	---	---	0.383	0.300	0.200	---	---
JEB	---	---	0.069	---	---	0.017	---	0.052	0.034	0.052	0.362	0.069	0.207	0.121	0.017	---
MHA	---	1.000	---	---	---	---	---	---	---	---	---	---	---	---	---	---
MHB	---	---	0.346	---	---	---	---	0.115	0.077	---	0.173	0.077	0.077	0.135	---	---
NAA	0.086	---	---	---	0.190	---	---	---	---	0.017	0.155	---	0.207	0.345	---	---
NAB	0.069	---	0.017	---	0.052	---	---	---	---	0.121	0.414	---	0.034	0.293	---	---
RGA	---	---	---	---	---	---	---	---	---	0.466	0.534	---	---	---	---	---
RGB	---	0.025	0.025	---	0.150	---	---	0.025	---	0.225	0.525	---	---	0.025	---	---
WCA	---	---	---	---	---	---	1.000	---	---	---	---	---	---	---	---	---
WCB	---	0.032	---	---	---	---	---	0.048	0.016	0.323	0.339	---	0.081	0.161	---	---
WFA	---	---	---	---	---	---	---	---	---	---	---	0.050	0.683	0.150	0.117	---
WFB	---	---	---	---	0.017	---	---	---	---	0.083	0.517	0.033	0.267	0.067	0.017	---
HLA	---	---	---	---	0.775	---	---	---	---	---	0.025	---	0.100	0.100	---	---
LPA	---	---	---	---	---	---	---	---	---	---	---	---	0.200	0.217	0.417	0.167
MAA	---	---	---	---	---	---	---	---	---	---	---	---	0.897	0.103	---	---
POA	---	---	---	---	---	---	---	---	---	---	0.167	---	0.833	---	---	---

APPENDIX 2 (continued). Allele frequencies at eight microsatellite loci in coastal cutthroat trout from isolated headwater streams in southeastern Alaska.

	OCL4														
	*58	*60	*70	*72	*74	*76	*78	*80	*82	*84	*86	*88	*90	*92	*96
DNA	---	---	---	---	---	0.037	0.093	0.019	---	0.315	0.315	0.222	---	---	---
DNB	---	0.016	---	---	0.097	0.048	0.677	---	---	0.032	---	0.113	0.016	---	---
DSA	---	---	---	---	---	---	1.000	---	---	---	---	---	---	---	---
DSB	---	0.024	---	---	0.071	---	0.833	---	---	0.048	---	0.024	---	---	---
JEA	---	---	---	---	0.250	---	0.567	---	0.183	---	---	---	---	---	---
JEB	0.034	0.069	0.069	---	0.190	0.017	0.517	---	0.034	---	---	---	0.052	0.017	---
MHA	---	---	---	---	---	---	1.000	---	---	---	---	---	---	---	---
MHB	---	0.038	---	---	0.019	---	0.750	---	0.096	---	---	---	---	---	0.096
NAA	0.017	---	---	---	0.017	---	0.190	---	---	0.172	---	0.603	---	---	---
NAB	0.086	0.034	---	---	0.103	---	0.328	0.017	---	0.017	---	0.414	---	---	---
RGA	---	1.000	---	---	---	---	---	---	---	---	---	---	---	---	---
RGB	---	0.350	---	---	---	---	0.525	---	---	---	---	0.050	0.075	---	---
WCA	---	---	---	---	---	---	1.000	---	---	---	---	---	---	---	---
WCB	0.016	0.032	---	---	0.032	0.016	0.774	---	---	---	0.032	0.048	0.048	---	---
WFA	---	---	---	---	1.000	---	---	---	---	---	---	---	---	---	---
WFB	---	0.034	---	---	0.052	---	0.534	0.207	---	0.017	0.034	0.103	0.017	---	---
HLA	0.100	---	0.150	---	0.175	---	0.500	---	0.075	---	---	---	---	---	---
LPA	---	---	---	0.517	---	---	0.483	---	---	---	---	---	---	---	---
MAA	---	---	---	---	---	---	0.815	---	0.019	---	0.056	0.111	---	---	---
POA	---	---	---	---	---	---	0.929	---	0.018	---	---	0.054	---	---	---

APPENDIX 2 (continued). Allele frequencies at eight microsatellite loci in coastal cutthroat trout from isolated headwater streams in southeastern Alaska.

	SFO8													
	*188	*196	*198	*200	*204	*206	*210	*212	*214	*218	*222	*224	*234	*236
DNA	---	0.583	---	---	---	---	0.117	0.300	---	---	---	---	---	---
DNB	---	0.576	0.015	---	---	---	0.167	0.167	---	0.061	0.015	---	---	---
DSA	---	0.404	---	---	---	---	0.538	---	---	0.058	---	---	---	---
DSB	---	0.571	---	---	---	---	0.238	0.095	---	0.095	---	---	---	---
JEA	---	---	---	---	---	---	0.850	---	---	---	0.150	---	---	---
JEB	---	0.293	---	0.034	---	---	0.328	0.138	---	0.017	0.172	0.017	---	---
MHA	---	---	---	---	---	---	0.447	---	---	---	---	---	0.553	---
MHB	0.196	0.130	0.087	---	---	---	0.348	---	---	---	0.239	---	---	---
NAA	---	0.121	---	---	---	---	0.793	0.034	0.052	---	---	---	---	---
NAB	---	0.707	---	---	---	---	0.086	0.155	0.017	---	0.034	---	---	---
RGA	---	---	---	---	---	---	---	---	---	---	0.315	---	---	0.685
RGB	---	0.075	0.100	---	---	---	0.300	0.100	---	0.025	0.200	---	---	0.200
WCA	---	1.000	---	---	---	---	---	---	---	---	---	---	---	---
WCB	---	0.250	---	---	---	---	0.411	0.179	---	0.018	0.143	---	---	---
WFA	---	---	---	---	---	---	---	0.720	0.280	---	---	---	---	---
WFB	---	0.417	---	0.017	---	---	0.250	0.283	---	---	0.033	---	---	---
HLA	---	---	---	0.147	0.353	---	0.500	---	---	---	---	---	---	---
LPA	---	---	---	---	---	0.091	0.886	---	0.023	---	---	---	---	---
MAA	---	---	---	---	---	0.033	0.967	---	---	---	---	---	---	---
POA	---	0.733	---	---	---	---	0.250	0.017	---	---	---	---	---	---

APPENDIX 2 (continued). Allele frequencies at eight microsatellite loci in coastal cutthroat trout from isolated headwater streams in southeastern Alaska.

	OCL2										
	*116	*136	*138	*142	*144	*146	*150	*152	*154	*156	*158
DNA	—	—	—	—	—	—	—	—	0.983	0.017	—
DNB	—	0.273	0.091	0.015	—	—	0.045	0.015	0.545	0.015	—
DSA	—	—	—	—	—	0.019	0.111	0.389	0.481	—	—
DSB	—	0.071	0.024	—	—	0.024	0.119	0.190	0.571	—	—
JEA	—	—	0.467	—	—	—	—	—	0.533	—	—
JEB	—	0.155	0.328	0.034	0.017	—	0.017	0.069	0.345	0.034	—
MHA	—	—	—	—	—	—	—	0.977	0.023	—	—
MHB	0.096	0.327	0.019	—	—	—	—	—	0.558	—	—
NAA	—	0.086	0.086	0.017	—	—	—	—	0.810	—	—
NAB	—	0.190	0.086	0.138	—	—	0.017	0.103	0.362	0.103	—
RGA	—	1.000	—	—	—	—	—	—	—	—	—
RGB	—	0.475	0.175	0.025	—	—	—	0.125	0.200	—	—
WCA	—	1.000	—	—	—	—	—	—	—	—	—
WCB	—	0.355	0.403	0.065	0.016	—	—	0.065	0.032	—	0.065
WFA	—	—	0.950	0.050	—	—	—	—	—	—	—
WFB	—	0.267	0.350	—	0.067	—	0.017	0.033	0.233	0.033	—
HLA	—	0.125	—	0.725	—	—	—	—	—	0.150	—
LPA	—	—	0.567	—	—	—	—	—	0.433	—	—
MAA	—	0.569	—	—	—	—	—	—	0.431	—	—
POA	—	0.183	0.017	—	—	—	—	—	0.800	—	—

APPENDIX 2 (continued). Allele frequencies at eight microsatellite loci in coastal cutthroat trout from isolated headwater streams in southeastern Alaska.

	OGO4										
	*132	*134	*136	*138	*140	*142	*144	*146	*148	*150	*152
DNA	—	—	—	—	0.100	—	—	—	0.400	0.500	—
DNB	—	0.106	—	—	0.152	0.061	0.015	—	0.424	0.242	—
DSA	—	0.222	—	—	—	—	—	—	0.463	0.315	—
DSB	—	0.214	0.071	—	0.238	—	—	0.024	0.214	0.214	0.024
JEA	—	—	—	—	—	0.200	—	—	0.800	—	—
JEB	—	0.103	—	—	0.034	0.172	—	—	0.586	0.052	0.052
MHA	—	—	—	—	0.750	—	—	0.250	—	—	—
MHB	—	0.038	—	—	—	0.596	—	0.308	0.058	—	—
NAA	—	—	—	—	—	—	—	0.138	0.828	0.034	—
NAB	—	0.121	0.310	0.017	0.052	—	—	0.052	0.310	0.138	—
RGA	—	—	—	—	—	—	—	—	0.672	—	0.328
RGB	—	0.175	—	—	0.100	—	—	—	0.600	—	0.125
WCA	—	—	—	—	1.000	—	—	—	—	—	—
WCB	0.274	—	0.016	—	0.145	—	0.048	—	0.323	0.048	0.145
WFA	—	—	—	—	—	—	—	—	1.000	—	—
WFB	0.050	0.083	0.017	—	0.017	0.033	—	0.067	0.517	0.183	0.033
HLA	—	—	—	—	0.875	—	—	0.100	0.025	—	—
LPA	—	—	0.433	—	—	—	—	—	0.567	—	—
MAA	0.034	—	0.845	—	—	—	—	—	0.121	—	—
POA	—	0.067	0.050	—	—	—	—	—	0.650	0.217	0.017

APPENDIX 2 (continued). Allele frequencies at eight microsatellite loci in coastal cutthroat trout from isolated headwater streams in southeastern Alaska.

	OCL1					
	*136	*140	*144	*148	*152	*156
DNA	---	0.283	0.333	0.267	---	0.117
DNB	---	0.333	0.424	0.212	---	0.030
DSA	---	0.093	0.500	0.407	---	---
DSB	---	0.071	0.619	0.262	---	0.048
JEA	---	---	---	0.550	0.150	0.300
JEB	---	0.259	0.379	0.328	---	0.034
MHA	---	---	1.000	---	---	---
MHB	---	0.577	0.365	0.058	---	---
NAA	0.241	0.293	0.431	---	---	0.034
NAB	0.017	0.172	0.621	0.190	---	---
RGA	---	0.069	---	0.931	---	---
RGB	---	0.125	0.275	0.375	0.175	0.050
WCA	---	1.000	---	---	---	---
WCB	---	0.274	0.500	0.161	0.065	---
WFA	---	---	1.000	---	---	---
WFB	---	0.250	0.533	0.150	0.033	0.033
HLA	---	---	0.075	0.925	---	---
LPA	---	1.000	---	---	---	---
MAA	---	---	1.000	---	---	---
POA	---	---	---	1.000	---	---

APPENDIX 2 (continued). Allele frequencies at eight microsatellite loci in coastal cutthroat trout from isolated headwater streams in southeastern Alaska.

	OGO8			
	*94	*96	*98	*100
DNA	—	0.833	0.117	0.050
DNB	0.076	0.379	0.227	0.318
DSA	0.519	—	0.444	0.037
DSB	0.405	0.048	0.429	0.119
JEA	—	0.083	0.917	—
JEB	0.241	0.138	0.466	0.155
MHA	—	1.000	—	—
MHB	—	0.096	0.731	0.173
NAA	0.086	0.034	0.655	0.224
NAB	0.345	—	0.517	0.138
RGA	—	—	0.086	0.914
RGB	0.250	0.075	0.175	0.500
WCA	—	—	1.000	—
WCB	0.339	0.081	0.306	0.274
WFA	0.433	0.183	0.383	—
WFB	0.283	0.217	0.200	0.300
HLA	0.650	0.250	—	0.100
LPA	—	1.000	—	—
MAA	0.500	—	—	0.500
POA	0.100	0.400	0.283	0.217

	ONEu11			
	*142	*144	*145	*146
DNA	0.417	0.583	—	—
DNB	0.091	0.909	—	—
DSA	—	1.000	—	—
DSB	0.024	0.786	0.190	—
JEA	—	1.000	—	—
JEB	0.034	0.828	0.138	—
MHA	—	0.727	0.273	—
MHB	0.173	0.827	—	—
NAA	—	0.655	0.345	—
NAB	0.017	0.914	0.069	—
RGA	—	0.293	0.707	—
RGB	—	0.550	0.450	—
WCA	—	1.000	—	—
WCB	0.048	0.935	0.016	—
WFA	—	—	1.000	—
WFB	0.050	0.933	0.017	—
HLA	—	0.900	0.100	—
LPA	—	1.000	—	—
MAA	—	1.000	—	—
POA	—	0.783	—	0.217

APPENDIX 3 – Accuracy of GIS-Mapped Stream Data

For larger drainages, we estimated stream lengths from the GIS database of stream reaches. We evaluated the accuracy of the GIS stream database for the smaller drainages where we measured stream length by surveying actual stream length on the ground (Figure A3.1). The correlation of mapped stream length with surveyed stream length is affected by: (1) errors of photointerpretation, *i.e.* drawing a stream channel in the wrong place; (2) missing smaller tributary channels that are not visible in aerial photographs; and (3) the fractal effect, whereby a the measured length of a convoluted pattern is positively correlated with the scale of measurement. The slope is not far from 1:1 and the regression is significant ($r^2 = .31$, $p = .01$), but there are clearly cases where photointerpretation overestimates or underestimates actual habitat amount by a factor of 2-3. Since we field-verified the length of shorter streams, where the likelihood of persistence was an open question, the uncertainty associated with GIS-based estimates of the length of longer streams did not especially influence our results. However, the presence of this uncertainty underscores the need to field-verify critical data derived from even high-quality GIS databases.

We found a similar pattern when comparing GIS-mapped barrier elevations with elevations taken in the field using a digital altimeter (Figure A3.2), for similar reasons. The correlation is again significant ($r^2 = .45$, $p = .00$), but there are obvious outliers. Unlike stream lengths, we did not systematically sample a particular stratum of barrier elevations, so the uncertainty associated with unverified barrier elevation estimates is randomly distributed. This uncertainty may have obscured somewhat the relationship

between isolation period, for which barrier elevation is a surrogate, and minimum habitat requirements for population persistence.

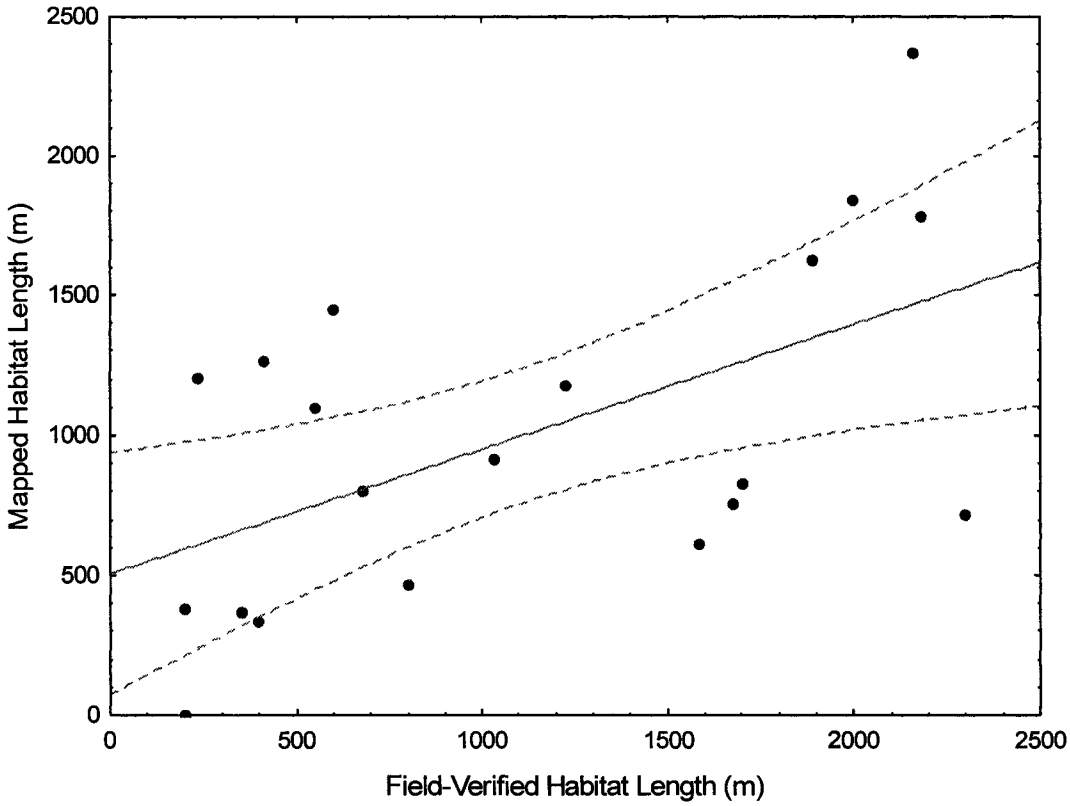

Figure A3.1. Relation of photointerpreted stream lengths to field-verified stream lengths for 19 smaller streams. (Field-verified lengths for streams longer than 2.5km are not available.)

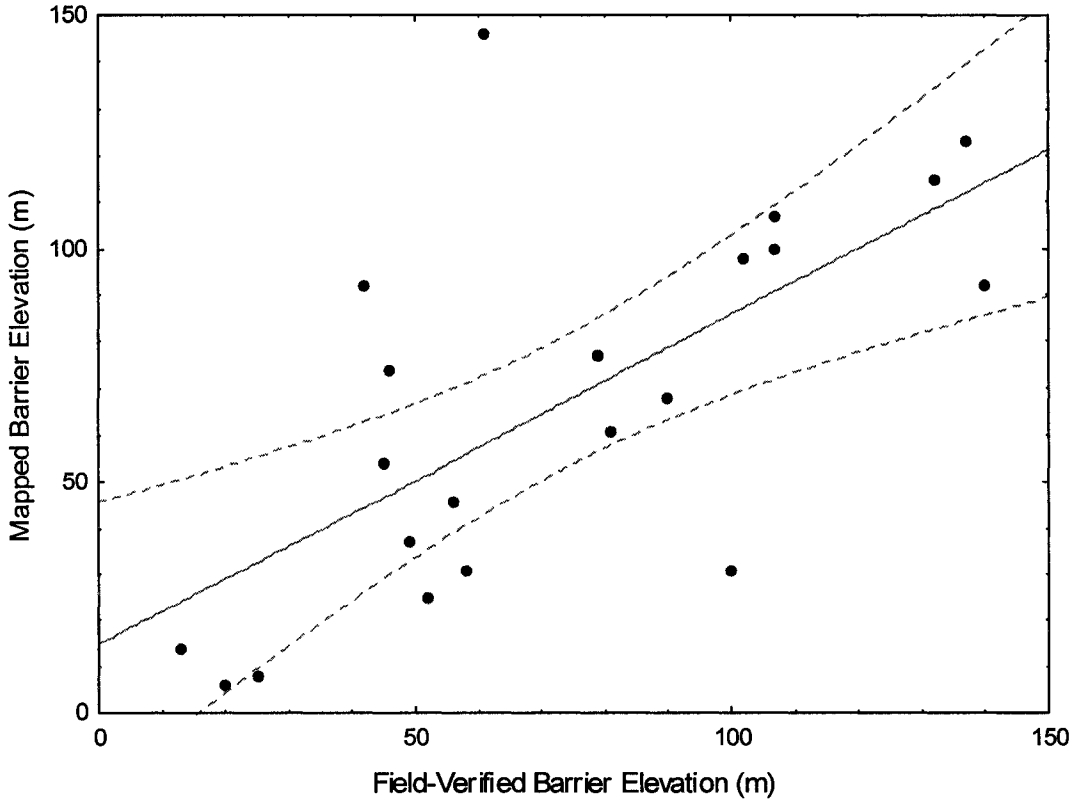

Figure A3.2. Relation of photointerpreted barrier elevations to field-verified barrier elevations for 21 streams.

APPENDIX 4. Sites where fish species presence above barriers was sampled. Drainage area is estimated from formula in Leopold et al. (1964). Isolation period is estimated using the regression developed in Chapter 2 (Figure 2.5).

Stream Name	*Zone*	*Habitat Length (m)*	*Drainage Area (ha)*	*Barrier Elevation (m ASL)*	*Isolation Period (years)*	*Coastal Cutthroat Trout*	*Dolly Varden*	*Verified (Barrier and Fish Species)*
S Fk Freshwater	Inner	50,100	2,109,700	69	9,000	Y	Y	Y
Portage	Inner	38,315	1,349,300	89	9,500	Y	Y	Y
N Arm Farragut	Mainland	28,900	843,300	15	6,200	Y	Y	Y
Tunehean	Inner	27,100	757,600	46	8,200	Y	Y	Y
rcs183	Outer	22,800	568,000	68	9,000	Y	Y	N
rcs086	Inner	19,500	437,700	38	7,900	Y	Y	N
rcs258	Outer	18,100	386,600	46	8,200	Y	Y	N
Zim	Inner	18,100	386,600	69	9,000	Y	Y	Y
rcs023	Inner	17,700	372,500	18	6,500	Y	Y	N
rcs169	Outer	16,800	341,500	43	8,100	Y	Y	N
W Fools	Inner	14,095	254,800	58	8,700	Y	Y	Y
Mason	Inner	13,455	235,800	61	8,800	Y	Y	Y
Packer	Inner	12,900	219,900	3	3,200	Y	Y	Y
rcs192	Inner	10,400	153,500	61	8,800	Y	Y	N
rcs477	Inner	9,200	125,200	31	7,500	Y	Y	N
East Fk Rowan Ck	Inner	7,910	97,300	43	8,100	Y	Y	Y
Dry Straits	Inner	7,775	94,500	15	6,200	Y	Y	Y
rcs422	Mainland	6,500	70,100	31	7,500	Y	Y	N
rcs061	Inner	6,000	61,400	46	8,200	Y	Y	N
Upper Corner	Inner	5,800	58,000	126	10,100	Y	Y	Y

Stream Name	*Zone*	*Habitat Length (m)*	*Drainage Area (ha)*	*Barrier Elevation (m ASL)*	*Isolation Period (years)*	*Coastal Cutthroat Trout*	*Dolly Varden*	*Verified (Barrier and Fish Species)*
Duncan	Inner	5,700	56,400	100	9,700	Y	Y	Y
Emerald	Inner	5,200	48,400	31	7,500	Y	Y	Y
rcs175	Outer	3,800	28,700	46	8,200	Y	Y	N
rcs458	Inner	3,700	27,400	84	9,400	Y	Y	N
Thoms Ck East	Inner	3,600	26,200	117	10,000	Y	Y	Y
rcs409	Mainland	3,400	23,800	61	8,800	Y	Y	N
rcs001	Inner	3,300	22,700	15	6,200	Y	Y	N
rcs084	Inner	3,200	21,500	95	9,600	Y	Y	N
Drinking Water	Inner	2,000	9,800	25	7,100	Y	Y	Y
rcs460	Inner	1,600	6,800	54	8,500	Y	Y	N
McHenry's Folly	Inner	1,500	6,100	52	8,500	Y	Y	Y
Jenkins	Mainland	1,400	5,400	130	10,200	Y	Y	Y
N Perkins	Inner	700	1,700	15	6,200	Y	Y	Y
rcs055	Inner	25,400	680,100	69	9,000	N	Y	N
rcs103	Inner	21,100	499,200	49	8,400	N	Y	N
Dry Bay	Mainland	20,900	491,400	31	7,500	N	Y	Y
rcs104	Inner	16,200	321,400	28	7,300	N	Y	N
rcs500	Inner	13,300	231,300	92	9,500	N	Y	N
West Hoya	Mainland	13,200	228,400	46	8,200	N	Y	Y
rcs210	Outer	13,100	225,600	84	9,400	N	Y	N
rcs285	Outer	11,800	189,500	54	8,500	N	Y	N
Keg	Inner	11,000	168,600	61	8,800	N	Y	Y
rcs161	Outer	10,800	163,500	68	9,000	N	Y	N
rcs495	Inner	10,400	153,500	31	7,500	N	Y	N
rcs282	Outer	10,000	143,800	31	7,500	N	Y	N

Stream Name	*Zone*	*Habitat Length (m)*	*Drainage Area (ha)*	*Barrier Elevation (m ASL)*	*Isolation Period (years)*	*Coastal Cutthroat Trout*	*Dolly Varden*	*Verified (Barrier and Fish Species)*
rcs017	Inner	8,600	111,900	80	9,300	N	Y	N
rcs094	Mainland	8,450	108,600	100	9,700	N	Y	N
Gunsight	Inner	8,300	105,400	123	10,100	N	Y	Y
rcs096	Inner	8,200	103,300	8	4,900	N	Y	N
rcs270	Outer	7,600	91,000	31	7,500	N	Y	N
Scat Ck	Inner	6,255	65,800	64	8,900	N	Y	Y
rcs397	Mainland	5,800	58,000	61	8,800	N	Y	N
Upper House Rock Ck	Inner	5,505	53,200	104	9,800	N	Y	Y
rcs097	Inner	5,300	49,900	103	9,800	N	Y	N
Upper Ohmer	Inner	5,200	48,400	177	10,800	N	Y	Y
Eagle River East	Mainland	5,100	46,800	77	9,200	N	Y	Y
Vial	Inner	4,900	43,800	58	8,700	N	Y	Y
rcs159	Outer	3,700	27,400	12	5,800	N	Y	N
Wilson Ck	Inner	3,675	27,100	54	8,500	N	Y	Y
Sheridan Ck	Inner	2,940	18,700	61	8,800	N	Y	Y
rcs459	Inner	2,700	16,200	84	9,400	N	Y	N
Canoe Pass	Inner	2,560	14,800	79	9,300	N	Y	Y
Upper Falls	Inner	2,275	12,200	173	10,700	N	Y	Y
Cairn	Inner	2,192	11,500	90	9,500	N	Y	Y
Little Dry Straits	Inner	2,000	9,800	137	10,300	N	Y	Y
rcs034	Inner	2,000	9,800	31	7,500	N	Y	N
Shockage Ck	Inner	1,580	6,600	107	9,800	N	Y	Y
rcs007	Inner	1,500	6,100	100	9,700	N	Y	N
Sun Luck Ck	Inner	1,330	5,000	55	8,600	N	Y	Y

Stream Name	*Zone*	*Habitat Length (m)*	*Drainage Area (ha)*	*Barrier Elevation (m ASL)*	*Isolation Period (years)*	*Coastal Cutthroat Trout*	*Dolly Varden*	*Verified (Barrier and Fish Species)*
rcs083	Inner	1,300	4,800	80	9,300	N	Y	N
rcs100	Inner	1,200	4,200	154	10,500	N	Y	N
W Fk Humbug Ck	Inner	530	1,100	23	6,900	N	Y	Y
rcs287	Outer	500	1,000	31	7,500	N	Y	N
Chantrelle Ck	Inner	414	700	46	8,200	N	Y	Y
rcs080	Inner	38,200	1,342,600	31	7,500	Y	N	N
rcs378	Inner	23,500	597,400	54	8,500	Y	N	N
Salty	Inner	22,500	555,600	34	7,700	Y	N	Y
rcs126	Outer	14,200	258,000	31	7,500	Y	N	N
rcs048	Inner	12,000	194,900	12	5,800	Y	N	N
rcs121	Outer	9,100	122,900	46	8,200	Y	N	N
rcs015	Inner	8,100	101,200	77	9,200	Y	N	N
Frenchy	Inner	4,890	43,700	150	10,500	Y	N	Y
Twin	Inner	4,720	41,200	92	9,500	Y	N	Y
Rugby	Inner	4,185	33,700	14	6,000	Y	N	Y
Gypsy	Mainland	4,100	32,500	58	8,700	Y	N	Y
Mystery	Inner	2,800	17,200	3	3,200	Y	N	Y
rcs070	Inner	2,600	15,200	89	9,500	Y	N	N
Montana	Mainland	2,400	13,300	1	1,100	Y	N	Y
rcs447	Mainland	2,400	13,300	61	8,800	Y	N	N
Leprechaun	Inner	2,370	13,100	138	10,300	Y	N	Y
rcs108	Outer	2,200	11,500	92	9,500	Y	N	N
rcs075	Inner	2,000	9,800	92	9,500	Y	N	N
Whitecap	Inner	1,585	6,700	81	9,300	Y	N	Y

Stream Name	*Zone*	*Habitat Length (m)*	*Drainage Area (ha)*	*Barrier Elevation (m ASL)*	*Isolation Period (years)*	*Coastal Cutthroat Trout*	*Dolly Varden*	*Verified (Barrier and Fish Species)*
rcs450	Inner	1,500	6,100	46	8,200	Y	N	N
rcs085	Inner	1,200	4,200	28	7,300	Y	N	N
rcs172	Outer	8,800	116,200	37	7,800	N	N	N
rcs402	Mainland	7,100	81,300	92	9,500	N	N	N
rcs199	Inner	3,100	20,400	23	6,900	N	N	N
Squirrel Ck	Inner	2,445	13,700	132	10,200	N	N	Y
Fishbuyer	Inner	2,300	12,400	102	9,700	N	N	Y
Bostwick	Inner	2,180	11,400	25	7,100	N	N	Y
rcs059	Inner	2,100	10,700	146	10,400	N	N	N
rcs196	Inner	2,000	9,800	92	9,500	N	N	N
Vallenar	Inner	1,891	9,000	20	6,700	N	N	Y
Fiftydollar	Inner	1,705	7,500	6	4,500	N	N	Y
rcs193	Inner	1,700	7,500	69	9,000	N	N	N
Rocky Kill	Inner	1,679	7,300	107	9,800	N	N	Y
rcs202	Inner	1,400	5,400	92	9,500	N	N	N
Harriman	Mainland	1,225	4,300	61	8,800	N	N	Y
Blank	Inner	1,035	3,300	58	8,700	N	N	Y
Fencepost Ck	Inner	800	2,100	45	8,200	N	N	Y
Driftwood Ck	Inner	705	1,700	43	8,100	N	N	Y
Little Anan Ck	Mainland	680	1,600	55	8,600	N	N	Y
MM Everest	Inner	617	1,400	100	9,700	N	N	Y
rcs448	Mainland	600	1,300	31	7,500	N	N	N
Slant Ck	Inner	600	1,300	68	9,000	N	N	Y
Vixen	Mainland	550	1,100	140	10,300	N	N	Y

Stream Name	*Zone*	*Habitat Length (m)*	*Drainage Area (ha)*	*Barrier Elevation (m ASL)*	*Isolation Period (years)*	*Coastal Cutthroat Trout*	*Dolly Varden*	*Verified (Barrier and Fish Species)*
rcs312	Inner	400	700	123	10,100	N	N	N
Rhubarb Ck	Inner	400	700	184	10,800	N	N	Y
Hannah's Ck	Inner	355	600	46	8,200	N	N	Y
Independence Ck	Inner	305	400	95	9,600	N	N	Y
Horsefly	Inner	235	300	49	8,400	N	N	Y
Africano Ck	Inner	200	200	84	9,400	N	N	Y
Backyard Ck	Inner	200	200	31	7,500	N	N	Y

APPENDIX 5. Estimates of fish density. Estimates were computed by Program MARK using three pass removal sampling data. An asterisk signifies that Program MARK was unable to compute an estimate from the data supplied for that year. Other years where data are missing were not sampled. A zero signifies that sampling was conducted but no fish of that species were detected.

Stream Name	*Reach Length (m)*	*Coastal Cutthroat Trout Density (fish/m)*						*Dolly Varden Density (fish/m)*					
		1999	*2000*	*2001*	*2002*	*2003*	*2004*	*1999*	*2000*	*2001*	*2002*	*2003*	*2004*
Drinking Water Cr	219	0.01	0.05	0.04	0.12	0.05	0.05	0.09	0.06	0.15	0.07	0.06	0.09
N Perkins Cr	165	0.11	0.10	0.11	0.15	0.20	0.27	0.07	0.12	0.02	0.07	0.07	0.11
Keg Cr	69	--	0.00	0.00	--	0.00	0.00	--	1.43	1.90	--	2.32	2.24
Montana Cr	120	0.26	0.33	0.35	0.61	0.41	0.37	0.00	0.00	0.00	0.00	0.00	0.00
Packer Cr	85	--	0.70	0.52	0.95	0.40	0.82	--	0.52	0.45	0.50	0.44	0.98
Gunsight Cr	124	--	0.00	0.00	0.00	0.00	0.00	--	1.71	2.66	2.88	4.26	5.42
Salty Cr	121	--	0.41	0.67	0.82	0.46	0.19	--	0.00	0.00	0.00	0.00	0.00
Emerald Cr	93	--	--	0.68	0.54	0.35	0.50	--	--	0.56	0.65	1.10	0.80
Gypsy Cr 1	146	0.23	0.22	0.50	0.29	0.21	0.24	0.00	0.00	0.00	0.00	0.00	0.00
Gypsy Cr 2	99	0.33	0.62	0.32	0.57	0.21	0.26	0.00	0.00	0.00	0.00	0.00	0.00
West Fork Hoya Cr	89	--	0.00	0.00	0.00	0.00	0.00	--	1.91	1.57	1.95	2.24	1.85
Vial Cr	158	--	0.00	0.00	0.00	0.00	0.00	--	0.90	0.56	1.04	1.08	0.76

	Reach Length (m)	*Coastal Cutthroat Trout Density (fish/m)*						*Dolly Varden Density (fish/m)*					
		1999	*2000*	*2001*	*2002*	*2003*	*2004*	*1999*	*2000*	*2001*	*2002*	*2003*	*2004*
Jenkins Cr	124	--	--	0.44	0.48	0.43	0.41	--	--	0.51	0.55	0.58	0.37
N Arm Farragut Cr	103	0.88	1.29	0.88	0.72	0.60	0.86	0.18	0.49	0.37	0.54	0.49	0.60
Upper Tunehean Cr	156	0.62	0.76	0.35	0.35	0.36	0.26	0.35	0.50	0.29	0.36	0.37	0.20
Lower Zim Cr	108	--	0.69	0.49	0.57	0.59	0.64	--	*	0.17	0.28	0.44	0.15
Upper Zim Cr	95	--	1.13	0.47	0.81	0.52	0.40	--	0.59	0.17	0.43	0.42	0.37
Ohmer Cr	149	--	--	0.00	0.00	0.00	0.00	--	--	0.34	0.89	0.88	1.51
Oxbow Cr	107	--	--	--	--	0.67	0.40	--	--	--	--	0.06	0.02
Scary Cr	128	--	--	--	--	--	0.00	--	--	--	--	--	0.96
Chanterelle Ck	122	--	--	--	--	--	0.00	--	--	--	--	--	0.48
S Fork Freshwater Cr	126	*	--	0.10	0.23	0.40	0.29	0.15	--	*	0.03	*	0.09
Upper Dry Bay Cr	131	--	--	0.00	--	0.00	--	--	--	1.27	--	1.14	--
Lower Dry Bay Cr	146	--	--	0.00	--	0.00	--	--	--	0.54	--	0.99	--

REFERENCES

Adams, S. B., C. A. Frissell, and B. E. Rieman. 2000. Movements of nonnative brook trout in relation to stream channel slope. Trans. Amer. Fish. Soc. **129**:623-638.

Alaback, P. B. 1982. Dynamics of understory biomass in Sitka spruce-western hemlock forests of southeast Alaska. Ecology **63**:1932-1948.

Alaback, P. B. 1995. Biodiversity patterns in relation to climate: the coastal temperate rainforests of North America. Pages 105-133 in R. G. Lawford, P. B. Alaback, and E. Fuentes, editors. High-latitude rainforests and associated ecosystems of the West Coast of the Americas: climate, hydrology, ecology, and conservation. Springer-Verlag, New York. 116.

Alaska Department of Fish and Game 2001. Summary of interagency discussions to develop a conceptual framework to evaluate the efficacy of terrestrial wildlife conservation measures of the Tongass Land Management Plan. On file with the Alaska Department of Fish and Game, Division of Wildlife Conservation, Juneau, Alaska.

Allendorf, F. W., D. Bayles, D. L. Bottom, K. P. Currens, C. A. Frissell, D. Hankin, J. A. Lichatowich, W. Nehlsen, P. C. Trotter, and T. H. Williams. 1997. Prioritizing Pacific salmon stocks for conservation. Cons. Bio. **11**:140-152.

Allendorf, F. W., and R. S. Waples. 1996. Conservation and genetics of salmonid fishes. Pages 238-280 in J. C. Avise, and J. L. Hamrick, editors. Conservation genetics: Case histories from nature. Chapman Hall, New York.

American Heritage Dictionaries 2000. The American Heritage Dictionary of the English Language, Fourth Edition. Houghton Mifflin, Boston, Massachusetts.

Arndt, K. L., R. H. Sackett, and J. A. Ketz 1987. A cultural resource overview of the Tongass National Forest, Alaska. Unpublished report. On file with USDA Forest Service, Juneau, Alaska.

Atkinson, A. J., P. C. Trenham, R. N. Fisher, S. A. Hathaway, B. S. Johnson, S. G. Torres, and Y. C. Moore 2004. Designing monitoring programs in an adaptive management context for regional multiple species conservation plans. U.S. Geological Survey Technical Report. USGS Western Ecological Research Center, Sacramento, California. 69 p. http://www.dfg.ca.gov/nccp/pubs/monframewk10-04.pdf.

Baichtal, J. 1999. Location, Sample Information, Elevation of 1999 C-14 Samples. Unpublished report. On file with Tongass National Forest, Thorne Bay, Alaska.

Baichtal, J. 2000. Location, Sample Information, Elevation of 2000 C-14 Samples. Unpublished report. On file with Tongass National Forest, Thorne Bay, Alaska.

Baichtal, J. 2001. Location, Sample Information, Elevation of 2001 C-14 Samples. Unpublished report. On file with Tongass National Forest, Thorne Bay, Alaska.

Bailey, R. G. 1995. Description of the ecoregions of the United States (2nd ed.). Misc. Pub. 1391, Map scale 1: 7,500,000. USDA Forest Service. 108 p.

Baker, T. T., A. C. Wertheimer, R. D. Burkett, R. Dunlap, D. M. Eggers, E. I. Fritts, A. J. Gharrett, R. A. Holmes, and R. L. Wilmot. 1996. Status of Pacific salmon and steelhead escapements in Southeastern Alaska. Fisheries **21**:6-18.

Barrie, J. V., and K. W. Conway. 1999. Late Quaternary glaciation and postglacial stratigraphy of the northern Pacific margin of Canada. Quaternary Research **51**:113-123.

Bayley, P. B., and L. L. Osborne. 1993. Naturla rehabilitation of stream fish populations in an Illinois catchment. Freshwater Biology **29**:295-300.

Beamish, R. J., and D. R. Bouillon. 1993. Pacific salmon production trends in relation to climate. Can. J. Fish. Aquat. Sci. **50**:1002-1016.

Beissinger, S. R. 2002. Population viability analysis: past, present, future. Page 577 in S. R. Beissinger, and D. R. McCullough, editors. Population viability analysis. University of Chicago Press, Chicago, Illinois.

Beissinger, S. R., and D. R. McCullough, editors. 2002. Population viability analysis. The University of Chicago Press, Chicago.

Bella, D. A. 1997. Organizational systems and the burden of proof. Pages 617-638 in D. J. Stouder, P. A. Bisson, and R. J. Naiman, editors. Pacific salmon and their ecosystems: status and future options. Chapman and Hall, New York.

Berg, H. C. 1973. Geology of Gravina Island, Alaska. Geological Survey Bulletin 1373. US Geological Survey, Washington, D.C.

Bevis, M., E. Kendrick, R. Smalley, R. Barriga, C. G., R. O'Connell, J. Normandeau, D. Angerman, and J. Klotz. 2002. Geodetic observation of postglacial rebound in Patagonia. Simposio International "Deformacion reciente de la corteza terrestre en Sudamerica y regiones adyacentes".

Bormann, B. T. 1994. Adaptive ecosystem management in the Pacific Northwest. General Technical Report PNW-GTR-341. USDA Forest Service, Pacific Northwest Research Station, Portland, Oregon. 22 p.

Brock, T., R. West, and S. J. Paustian 1996. Landforms of the Alaska Region classification guide. Unpublished manuscript. On file with USDA Forest Service, Alaska Region, Juneau, Alaska.

Brown, J. H. 1995. Macroecology. University of Chicago Press, Chicago.

Brown, J. H., and A. Kodric-Brown. 1977. Turnover rates in insular biogeography: effect of immigration on extinction. Ecology **58**:445-449.

Bryant, M. D. 2002. Estimating fish populations by removal methods with minnow traps in southeast Alaska streams. N. Amer. J. Fish. Mgmt. **20**.

Bryant, M. D., R. T. Edwards, and R. D. Woodsmith. *in press*. An approach to effectiveness monitoring of floodplain channel aquatic habitat: salmonid relationships. Landscape and Urban Planning.

Bryant, M. D., N. D. Zymonas, and B. E. Wright. 2004. Salmonids on the fringe: abundance, species composition, and habitat use of salmonids in high gradient headwater streams, Southeast Alaska. Trans. Amer. Fish. Soc. **133**:1529-1538.

Buddington, A. F. 1927. Abandoned marine benches in southeastern Alaska. Am. Journ. Sci. **8**:45-52.

Buskirk, S. W., and R. A. Powell. 1994. Habitat ecology of fishers and American martens. Pages 283-296 in S. W. Buskirk, A. S. Harestad, M. G. Raphael, and R. A. Powell, editors. Martens, sables, and fishers: biology and conservation. Cornell University Press, Ithaca, New York.

Carlsson, J., and J. Nilsson. 2001. Effects of geomorphological structures on genetic differentiation among brown trout populations in a northern boreal river drainage. Trans. Amer. Fish. Soc. **130**:36-45.

Caro, T. M., and G. O'Doherty. 1999. On the use of surrogate species in conservation biology. Cons. Bio. **13**:805-813.

Carrara, P. E., T. A. Ager, J. F. Baichtal, and D. Van Sistine. 2002. Late Wisconsin glacial limits in southern southeastern Alaska, as indicated by a new bathymetric map. 32nd Annual Arctic Workshop Abstracts, March 14-16, 2002, INSTAAR, University of Colorado, Boulder, Colorado.

Castric, V., F. Bonney, and L. Bernatchez. 2001. Landscape structure and hierarchical genetic diversity in the brook charr, *Salvelinus fontinalis*. Evolution **55**:1016-1028.

Caughley, G. 1994. Directions in conservation biology. Journal of Animal Ecology **63**:215-244.

Clague, J. J. 1989. Quaternary sea levels. Pages 43-45 in R. J. Fulton, editor. Quaternary geology of Canada and Greenland. Geological Survey of Canada, Geology of Canada, no. 1. (Also Geological Survey of America, The geology of America, v. K-1.).

Clague, J. J., J. R. Harper, R. J. Hebda, and D. E. Howes. 1982. Late Quaternary sea levels and crustal movements, coastal British Columbia. Can. J. Earth. Sci. **19**:597-618.

Condrey, M. J., and P. Bentzen. 1998. Characterization of coastal cutthroat trout (*Oncorhynchus clarki clarki*) microsatellites and their conservation in other salmonids. Molecular Ecology **7**:787-788.

Cook, J. A., A. L. Bidlack, C. J. Conroy, J. R. Demboski, M. A. Fleming, A. M. Runck, K. D. Stone, and S. O. MacDonald. 2001. A phylogenetic perspective on

endemism in the Alexander Archipelago of southeast Alaska. Biological Conservation **97**:215-227.

Costello, A. B., T. E. Down, M. Pollard, C. J. Pacas, and E. B. Taylor. 2003. The influence of history and contemporary stream hydrology on the evolution of genetic diversity within species: an examination of microsatellite DNA variation in bull trout, *Salvelinus confluentus* (Pisces: Salmonidae). Evolution **57**:328-344.

Crow, J. F., and M. Kimura 1970. An introduction to population genetics theory. Harper and Row, New York.

Currens, K. P., C. B. Schreck, and H. W. Li. 1990. Allozyme and morphological divergence of rainbow trout (*Oncorhynchus mykiss*) above and below waterfalls in the Deschutes River, Oregon. Copeia:730-746.

Demboski, J. R., K. R. Stone, and J. A. Cooak. 1999. Further perspectives on the Haida Gwaii glacial refugium. Evolution **53**:2008-2012.

Dolloff, C. A., and G. H. Reeves. 1990. Microhabitat partitioning among stream-dwelling juvenile coho salmon, *Oncorhynchus kisutch*, and Dolly Varden, *Salvelinus malma*. Can. J. Fish. Aquat. Sci. **47**:2297-2306.

Dunham, J. B., and B. E. Rieman. 1999. Metapopulation structure of bull trout: influences of physical, biotic, and geometrical landscape characteristics. Ecol. Appl. **9**:642-655.

Dunning, J. B., B. J. Danielson, and H. R. Pulliam. 1992. Ecological processes that affect populations in complex landscapes. Oikos **65**:169-175.

Durbin, K. 1999. Tongass: pulp politics and the fight for the Alaska rain forest. Oregon State University Press, Corvallis, Oregon.

Everest, F. H. *in press*. Setting the stage for the development of a science-based Tongass land management plan. Landscape and Urban Planning.

Everest, F. H., J. C. Capp, J. L. Kershner, and M. A. Brookes 1995. Report to congress: anadromous fish habitat assessment. Publication R10-MB-279. USDA Forest Service, Pacific Northwest Research Station, Alaska Region, Juneau, Alaska.

Fahrig, L. 2001. How much habitat is enough? Biological Conservation **100**:65-74.

Fahrig, L. 2003. Effects of habitat fragmentation on biodiversity. Annual Review of Ecology, Evolution and Systematics **34**:487-515.

Fairbanks, R. G. 1989. A 17,000-year glacio-eustatic sea level record: influence of glacial melting rates on the Younger Dryas event and deep-ocean circulation. Nature **342**:637-642.

Frankham, R. 1995a. Conservation genetics. Ann. Rev. Gen. **29**:305-327.

Frankham, R. 1995b. Effective population size/adult population size ratios in wildlife: a review. Genetical Research **66**:95-107.

Frankham, R. 1996. Relationship of genetic variation to population size in wildlife. Cons. Bio. **10**:1500-1508.

Franklin, I. R. 1980. Evolutionary change in small populations. Pages 135-149 in M. E. Soule, and B. A. Wilcox, editors. Conservation biology: an evolutionary-ecological perspective. Sinauer, Sunderland, Massachusetts.

Franklin, I. R., and R. Frankham. 1998. How large must populations be to retain evolutionary potential? Animal Conservation **1**:69-70.

Franklin, J. F. 1993. Preserving biodiversity: species, ecosystems, or landscapes? Ecol. Appl. **3**:202-205.

Funk, W. C. 2004. Patterns and consequences of dispersal in Columbia spotted frogs (*Rana luteiventris*). Unpublished Ph.D. dissertation, The University of Montana, Missoula, Montana.141 pages.

Gilpin, M. E., and M. E. Soule. 1986. Minimum viable populations: processes of species extinction. Pages 135-149 in M. E. Soule, editor. Conservation biology: the science of scarcity and diversity. Sinauer Associates, Sunderland, Massachusetts.

Glova, G. J. 1987. Comparison of allopatric cutthroat trout stocks with those sympatric with coho salmon and sculpins in small streams. Env. Biol. Fish. **20**:275-284.

Goudet, J. 2001. FSTAT, a program to estimate and test gene diversities and fixation indices (version 2.9.3). Available from http://www.unil.ch/izea/softwares/fstat.html. Updated from Goudet (1995).

Harig, A. L., and K. D. Fausch. 2002. Minimum habitat requirements for establishing translocated cutthroat trout populations. Ecol. Appl. **12**:535-551.

Hastings, K. 2005. Long-term persistence of isolated fish populations in the Alexander Archipelago. Unpublished Ph.D. dissertation, Division of Biological Sciences, University of Montana, Missoula, Montana.

Hearn, W. E. 1987. Interspecific competition and habitat segregation among stream-dwelling trout and salmon: a review. Fisheries **12**:24-31.

Heaton, T. H., S. L. Talbot, and G. F. Shields. 1996. An ice age refugium for large mammals in the Alexander Archipelago, southeastern Alaska. Quaternary Research **46**:186-192.

Heusser, C. J. 1989. North Pacific coastal refugia -- the Queen Charlotte Islands in perspective. Pages 91-106 in G. G. E. Scudder, and N. Gessler, editors. The outer

shores. Based on the proceedings of the Queen Charlotte Islands first international scientific symposium, University of British Columbia, August 1984. Queen Charlotte Islands Museum Press, Queen Charlotte City, B.C.

Hicks, S. D., and W. Shofnos. 1965. The determination of land emergence from sea level observations in Southeast Alaska. Journal of Geophysical Research **70**:3315-3320.

Hilderbrand, R. H., and J. L. Kershner. 2000. Conserving inland cutthroat trout in small streams: how much stream is enough? N. Amer. J. Fish. Mgmt. **20**:513-520.

Hitt, N. P., C. A. Frissell, C. C. Muhlfeld, and F. W. Allendorf. 2003. Spread of hybridization between native westslope cutthroat trout, *Oncorhynchus clarki lewisi*, and nonnative rainbow trout, *Oncorhynchus mykiss*. Can. J. Fish. Aquat. Sci. **60**:1440-1451.

Hobbie, J. E., S. R. Carpenter, N. B. Grimm, J. R. Gosz, and T. R. Seastedt. 2003. The US Long Term Ecological Research Program. Bioscience **53**:21-32.

Holtby, L. B., and J. C. Scrivener. 1989. Observed and simulated effects of climatic variability, clear-cut logging and fishing on the numbers of chum salmon (*Oncorhynchus keta*) and coho salmon (*O. kisutch*) returning to Carnation Creek, British Columbia. Pages 62-81 in C. D. Levings, L. B. Holtby, and M. A. Henderson, editors. Proceedings of the national workshop on effects of habitat alteration on salmonid stocks. Can. Spec. Publ. Fish. Aquat. Sci. 105.

Husband, B. B., and S. C. H. Barrett. 1992. Effective population size and genetic drift in tristylous *Eichhornia paniculata* (Pontederiaceae). Evolution **46**:1875-1890.

Iverson, G. C., G. D. Hayward, K. Titus, E. DeGayner, R. Lowell, D. C. Crocker-Bedford, P. F. Schempf, and J. Lindell 1996. Conservation assessment for the northern goshawk in Southeast Alaska. General Technical Report PNW-GTR-387. USDA Forest Service, Pacific Northwest Research Station, Portland, Oregon. 101 p.

Ives, P. C., B. Levin, C. L. Oman, and M. Rubin. 1967. U.S. Geological Survey Radiocarbon Dates IX. Radiocarbon **9**:505-529.

Ivins, E. R., and T. James. 1999. Simple models for late Holocene and present-day Patagonian glacier fluctuations and predictions of a geodetically detectable isostatic response. Geophysical Journal International **138**:601-624.

Johnson, B. L. 1999. The role of adaptive management as an operational approach for resource management agencies. Cons. Ecol. **3**:8. [online] URL: http://www.consecol.org/vol3/iss2/art8.

Johnson, O. W., M. H. Ruckelshaus, W. S. Grant, F. W. Waknitz, A. M. Garrett, G. J. Bryant, K. Neely, and J. J. Hard 1999. Status review of coastal cutthroat trout from Washington, Oregon, and California. NOAA Tech. Memo. NMFS-NWFSC-37. U.S. Dept. of Commerce.

June, J. A. 1981. Life history and habitat utilization of cutthroat trout (*Salmo clarki*) in a headwater stream on the Olympic Peninsula. Unpublished M.S. thesis, University of Washington, Seattle, Washington.112 pages.

Kahler, T. H., and T. P. Quinn 1998. Juvenile and resident salmonid movement through culverts. Final Report. WA-RD 457.1. Washington State Department of Transportation, Seattle, Washington.

Kalinowski, S. T., and R. S. Waples. 2002. The relationship of effective to census population size in fluctuating populations. Cons. Bio. **16**:1-9.

Kanda, N., R. F. Leary, P. Spruell, and F. W. Allendorf. 2002. Molecular genetic markers identifying hybridization between the Colorado River greenback cutthroat trout complex and Yellowstone cutthroat trout or rainbow trout. Trans. Amer. Fish. Soc. **131**:312-319.

Kiester, A. R., and C. Eckhardt 1994. Review of wildlife management and conservation biology on the Tongass National Forest: a synthesis with recommendations. USDA Forest Service, Pacific Northwest Research Station, Corvallis, OR. 282 p.

Klein, D. R. 1965. Postglacial distribution patterns of mammals in the southern coastal regions of Alaska. Arctic **18**:7-20.

Koizumi, I., and K. Maekawa. 2004. Metapopulation structure of stream-dwelling Dolly Varden charr inferred from patterns of occurrence in the Sorachi River basin, Hokkaido, Japan. Freshwater Biology.

Kruse, C. G., W. A. Hubert, and F. J. Rahel. 2001. An assessment of headwater isolation as a conservation strategy for cutthroat trout in the Absaroka Mountains of Wyoming. Northwest Science **75**:1-10.

Landres, P. B., J. Verner, and J. W. Thomas. 1988. Ecological uses of vertebrate indicator species: a critique. Cons. Bio. **2**:316-328.

Larimore, R. W., W. F. Childers, and C. Heckrotte. 1959. Destruction and reestablishment of stream fish and invertebrates affected by drought. Trans. Amer. Fish. Soc. **88**:261-285.

Lemke, R. W. 1975. Reconnaissance engineering geology of the Ketchikan Area, Alaska, with emphasis on evaluation of earthquake and other geologic hazards. Open File Report 75-250. US Geological Survey. 65 p.

Lemke, R. W., and L. A. Yehle 1972. Reconnaissance engineering geology of the Haines Area, Alaska, with emphasis on evaluation of earthquake and other geologic hazards. Open File Report [no number included]. US Geological Survey. 99 p.

Leopold, L. B., M. G. Wolman, and J. P. Miller 1964. Fluvial processes in geomorphology. W.H. Freeman and Company, San Francisco.

Lynch, M., and R. Lande. 1998. The critical effective size for a genetically secure population. Animal Conservation **1**:70-72.

Mann, D. 1986. Wisconsin and Holocene glaciation of Southeast Alaska. Pages 237-265 in T. D. Hamilton, K. M. Reed, and R. M. Thorson, editors. Glaciation in Alaska, the geologic record. Alaska Geological Society, Anchorage, Alaska.

Mann, D. H., and T. D. Hamilton. 1995. Late pleistocene and holocene paleoenvironments of the North Pacific coast. Quaternary Science Reviews **14**:449-471.

Margules, C. R., and R. L. Pressey. 2000. Systematic conservation planning. Nature **405**:243-253.

Martin-Smith, K. M., and L. M. Laird. 1998. Depauperate freshwater fish communities in Sabah: the role of barriers to movement and habitat quality. J. Fish Biol. **53**:331-344.

McGlashan, D. J., and M. Hughes. 2000. Reconciling patterns of genetic variation with stream structure, earth history and biology in the Australian freshwater fish

Craterocephalus stercusmuscarum (Atherinidae). Molecular Ecology **9**:1737-1751.

McPhail, J. D., and C. C. Lindsey. 1986. Zoogeography of the freshwater fishes of Cascadia (the Columbia System and rivers north to the Stikine). Pages 615-637 in C. H. Hocutt, and E. O. Wiley, editors. The zoogeography of North American freshwater fishes. John Wiley and Sons, New York, NY.

Meffe, G. K., and A. L. Sheldon. 1990. Post-defaunation recovery of fish assemblages in southeastern (South Carolina, USA) blackwater streams. Ecology **71**:657-667.

Michener, W. K., J. B. Brunt, J. J. Helly, T. B. Kirchner, and S. G. Stafford. 1997. Nongeospatial metadata for the ecological sciences. Ecol. Appl. **7**:330-342.

Michener, W. K., J. H. Porter, and S. G. Stafford 1998. Data and information management in the ecological sciences: a resource guide. LTER Network Office, University of New Mexico, Albuquerque, New Mexico.

Miller, R. D. 1972. Surficial geology of the Juneau urban area and vicinity, Alaska, with emphasis on earthquake and other geologic hazards. Open File Report 72-255. US Geological Survey. 108 p.

Miller, R. D. 1973a. Gastineau channel formation, a composite glaciomarine deposit near Juneau, Alaska. Geological Survey Bulletin 1394-C. US Geological Survey, Washington, D.C. 20 p.

Miller, R. D. 1973b. Two diamictons in a landslide scarp on Admiralty island, Alaska, and the tectonic insignificance of an intervening peat bed. Journal of Research of the U.S. Geological Survey **1**:309-314.

Mills, L. S. 1995. Edge effects and isolation: red-backed voles on forest remnants. Cons. Bio. **9**:395-403.

Mills, L. S., and F. W. Allendorf. 1996. The one-migrant-per-generation rule in conservation and management. Cons. Bio. **10**:1509-1518.

Mills, T. J., F. H. Everest, P. Janik, B. Pendleton, C. G. Shaw III, and D. N. Swanston. 1998. Science/management collaboration: lessons learned from the revision of the Tongass National Forest Plan. Western Journal of Applied Forestry **13**:90-96.

Milner, A. M., and R. G. Bailey. 1989. Salmonid colonization of new streams in Glacier Bay National Park, Alaska. Aquaculture and Fisheries Management **20**:179-192.

Milner, A. M., E. E. Knudsen, C. Soiseth, A. L. Robertson, D. Schell, I. T. Phillips, and K. Magnusson. 2000. Colonization and development of stream communities across a 200 year gradient in Glacier Bay National Park, Alaska, USA. Pages 2319-2335. Can. J. Fish. Aquat. Sci.

Mobley, C. M. 1988. Holocene sea levels in southeast Alaska: preliminary results. Arctic **41**:261-266.

Montgomery, M. E., L. M. Woodworth, R. K. Nurthen, D. M. Gilligan, D. A. Briscoe, and R. Frankham. 2000. Relationships between population size and loss of genetic diversity: comparisons of experimental results with theoretical predictions. Conservation Genetics **1**:33-43.

Moodie, G. E. E., and T. E. Reimchen. 1976. Glacial refugia, endemism, and stickleback populations of the Queen Charlotte Islands, British Columbia. Canadian Field-Naturalist **90**.

Morita, K., and S. Yamamoto. 2002. Effects of habitat fragmentation by damming on the persistence of stream-dwelling charr populations. Cons. Bio. **16**:1318-1325.

Morris, W. F., and D. F. Doak 2003. Quantitative conservation biology: theory and practice of population viability analysis. Sinauer Associates, Sunderland, Massachusetts.

Morrow, J. E. 1980. Freshwater fishes of Alaska. Alaska Northwest Publishing, Anchorage, Alaska.

Newman, D., and D. A. Tallmon. 2001. Experimental evidence for beneficial fitness effects of gene flow in recently isolated populations. Cons. Bio. **15**:1054-1063.

Newnham, R. M., D. J. Lowe, and P. W. Williams. 1999. Quaternary environmental change in New Zealand: a review. Progress in Physical Geography **23**:567-610.

Niemi, G. J., J. M. Hanowski, A. R. Lima, T. Nicholls, and N. Weilland. 1997. A critical analysis on the use of indicator species in management. Journal of Wildlife Management **61**:1240-1252.

Northcote, T. G. 1995. Confessions from a four decade affair with Dolly Varden: a synthesis and critique of experimental tests for interactive segregation between Dolly Varden char (*Salvelinus malma*) and cutthroat trout (*Oncorynchus clarki*) in British Columbia. Nordic J. Freshw. Res. **71**:49-67.

Noss, R. F., and A. Y. Cooperrider 1994. Saving nature's legacy: protecting and restoring biodiversity. Island Press, Washington, D.C.

Novinger, D. C., and F. J. Rahel. 2003. Isolation management with artificial barriers as a conservation strategy for cutthroat trout in headwater streams. Cons. Bio. **17**:772-781.

Nowacki, G., P. Krosse, G. Fisher, D. Brew, T. Brock, M. Shephard, W. Pawuk, J. Baichtal, and E. Kissinger 2001. Ecological Subsections of southeast Alaska and neighboring areas of Canada. Technical Publication R10-TP-75. USDA Forest Service, Alaska Region.

Nozawa, K. 1963. Competition between brown gene and its wild-type allele in *Drosophila melanogaster*. II. Estimation of relative viability of brown homozygotes and an analysis of changes in gene-frequency. Japanese Journal of Genetics **38**:6-20.

Nozawa, K. 1970. Estimation of the effective size in *Drosophila* experimental populations. Drosophila Information Service **45**:117-118.

Nyberg, J. B., and B. Taylor. 1995. Applying adaptive management in British Columbia's forests. Pages 239-245. Proceedings of the FAO/ECE/ILO International Forestry Seminar, September 9-15, 1995. Canadian Forest Service, Prince George, British Columbia.

Oliver, C. D., and B. C. Larson 1996. Forest stand dynamics. Wiley Publishing, Indianapolis, Indiana.

Palmer, C. J. 2003. Approaches to quality assurance and information management for regional ecological monitoring programs. Page 447 in D. E. Busch, and J. C. Trexler, editors. Monitoring ecosystems: interdisciplinary approaches for evaluating ecoregional initiatives. Island Press, Washington D.C.

Pawuk, W. H., and E. J. Kissinger 1989. Preliminary forest plant associations of the Stikine Area, Tongass National Forest. Technical Paper R10-TP-72. USDA Forest Service, Alaska Region, Juneau, Alaska.

Peltier, W. R. 1994. Ice age paleotopography. Science **265**:195-197.

Person, D. K., M. D. Kirchhoff, V. van Ballenberghe, G. C. Iverson, and E. Grossman 1996. The Alexander Archipelago wolf: a conservation assessment. General Technical Report PNW-GTR-384. USDA Forest Service, Pacific Northwest Research Station, Portland, Oregon.

Pielou, E. C. 1991. After the ice age: the return of life to glaciated North America. University of Chicago Press, Chicago.

Pister, E. P. 1985. Desert pupfishes: reflections on reality, desirability, and conscience. Env. Biol. Fish. **12**:3-11.

Poiani, K. A., B. D. Richter, M. A. Anderson, and H. E. Richter. 2000. Biodiversity conservation at multiple scales: functional sites, landscapes, and networks. Bioscience **50**:133-146.

Pray, L. A., C. J. Goodnight, L. Stevens, J. M. Schwartz, and G. Yan. 1996. The effect of population size on effective population size: an empirical study in the red flour beetle *Tribolium castaneum*. Genetical Research **68**:151-155.

Reed, J. C., and R. R. Coats 1941. Geology and ore deposits of the Chichagof mining district Alaska. Bulletin 929. US Geological Survey, Washington, D.C.

Rexstad, E., and K. P. Burnham 1991. Users guide for interactive program CAPTURE. Colorado Cooperative Fish & Wildlife Research Unit, Colorado State University, Fort Collins, Colorado.

Rice, W. R. 1989. Analysing tables of statistical tests. Evolution **43**:223-225.

Riddihough, R. P. 1982. Contemporary movements and tectonics on Canada's west coast: a discussion. Tectonophysics **86**:319-341.

Rieman, B. E., D. Lee, J. D. McIntyre, K. Overton, and R. Thurow 1993. Consideration of extinction risks for salmonids. Fish Habitat Relationships Technical Bulletin No. 14. USDA Forest Service.

Ringold, P. L., J. Alegria, R. L. Czaplewski, B. S. Mulder, T. Tolle, and K. Burnett. 1996. Adaptive monitoring design for ecosystem management. Ecol. Appl. **6**:745-747.

Rogers, R. A., L. D. Martin, and T. D. Nicklas. 1990. Ice-age geography and the distribution of native North American languages. J. Biogeography **17**:131-143.

Sainsbury, C. L. 1961. Geology of part of the Craig C-2 quadrangle and adjoining areas Prince of Wales Island, Southeastern Alaska. Geological Survey Bulletin 1058-H. US Geological Survey, Washington, D.C.

Schmidt, A. E. 1997. Status of sea-run cutthroat trout stocks in Alaska. Pages 80-83 in J. D. Hall, P. A. Bisson, and R. E. Gresswell, editors. Sea-run cutthroat trout: biology, management, and future conservation. Oregon Chapter, American Fisheries Society, Corvallis, Oregon.

Schoonmaker, P., and W. Luscombe 2005. Habitat monitoring: an approach for reporting status and trends for state comprehensive wildlife conservation strategies. Report prepared for Defenders of Wildlife, Portland, Oregon. http://www.biodiversitypartners.org/infomanage/monitoring/01.shtml.

Senanan, W., and A. R. Kapuscinski. 2000. Genetic relationships among populations of northern pike (*Esox lucius*). Can. J. Fish. Aquat. Sci. **57**:391-404.

Shaffer, M. L. 1981. Minimum population sizes for species conservation. Bioscience **31**:131-134.

Shaw, C. G., III 1999. Use of risk assessment panels during revision of the Tongass Land and Resource Management Plan. Publication R10-MB 460. USDA Forest Service, Pacific Northwest Research Station, Portland, Oregon.

Shea Flanders, L., and J. Cariello 2000. Tongass road condition survey report. Technical Report No. 00-7. Alaska Department of Fish and Game, Habitat and Restoration Division, Douglas, Alaska.

Shennan, I., and B. Horton. 2002. Holocene land and sea level changes in Great Britain. Journal of Quaternary Science **17**:511-526.

Simberloff, D. A. 1998. Flagships, umbrellas, and keystones: is single species management passe in the landscape era? Biological Conservation **83**:247-257.

Slaney, T. L., K. D. Hyatt, T. G. Northcote, and R. J. Fielden. 1996. Status of anadromous salmon and trout in British Columbia and Yukon. Fisheries **21**:20-35.

Smith, W. P. *in prep.* Problem analysis: maintaining well-distributed, viable populations of indigenous vertebrate species in the Tongass National Forest.

Smith, W. P. *in press*. Evolutionary diversity and ecology of endemic small mammals of southeastern Alaska with implications for land management planning. Landscape and Urban Planning.

Soule, M. E. 1976. Allozyme variation: its determinants in space and time. Pages 60-77 in F. J. Ayala, editor. Molecular evolution. Sinauer Associates, Sunderland, Massachusetts.

Soule, M. E., and J. Terborgh, editors. 1999. Continental conservation: scientific foundations of regional reserve networks. Island Press, Washington, D.C.

Soule, M. E., and B. A. Wilcox, editors. 1980. Conservation biology: an evolutionary-ecological perspective. Sinauer, Sunderland, Massachusetts.

Spruell, P., M. L. Bartron, N. Kanda, and F. W. Allendorf. 2001. Detection of hybrids between bull trout (*Salvelinus confluentus*) and brook trout (*Salvelinus fontinalis*) using PCR primers complementary to interspersed nuclear elements. Copeia **2001(4)**:1093-1099.

Steidl, R. J., J. P. Hayes, and E. Schauber. 1997. Statistical power analysis in wildlife research. Journal of Wildlife Management **61**:270-279.

Stouder, D. J., P. A. Bisson, and R. J. Naiman, editors. 1997. Pacific salmon and their ecosystems: status and future options. Chapman and Hall, New York.

Strickland, M. D., H. J. Harju, K. R. McCaffery, H. W. Miller, L. M. Smith, and R. J. Stoll. 1996. Harvest management. Pages 445-483 in T. A. Bookhout, editor. Research and management techniques for wildlife and habitats. Fifth ed., rev. The Wildlife Society, Bethesda, Maryland.

Stuiver, M., and H. A. Polach. 1977. Discussion: reporting of ^{14}C data. Radiocarbon **19**:355-363.

Suring, L. A., D. C. Crocker-Bedford, R. W. Flynn, C. S. Hale, G. C. Iverson, M. D. Kirchhoff, T. E. Schenck II, L. C. Shea, and K. Titus 1993. A proposed strategy for maintaining well-distributed, viable populations of wildlife associated with old-growth forests in Southeast Alaska. Publication R10-MB 478. USDA Forest Service, Alaska Region, Juneau, Alaska. 278 p.

Suring, L. A., D. C. Crocker-Bedford, R. W. Flynn, C. S. Hale, G. C. Iverson, M. D. Kirchhoff, T. E. Schenck II, L. C. Shea, and K. Titus 1994. Response to the peer

review of: a proposed strategy for maintaining well-distributed, viable populations of wildlife associated with old-growth forests in Southeast Alaska. USDA Forest Service, Alaska Region, Juneau, Alaska. 11 p.

Swales, S., and C. D. Levings. 1989. Role of off-channel ponds in the life cycle of coho salmon (*Oncorhynchus kisutch*) and other juvenile salmonids in the Coldwater River, British Columbia. Can. J. Fish. Aquat. Sci. **46**:232-242.

Tallmon, D. A. 2001. Genetic, demographic, and ecological effects of habitat fragmentation. Unpublished Ph.D. dissertation, The University of Montana, Missoula, Montana.159 pages.

Tallmon, D. A., H. M. Draheim, L. S. Mills, and F. W. Allendorf. 2002. Insights into recently fragmented vole populations from combined genetic and demographic data. Molecular Ecology **11**:699-709.

Taylor, B. L., and T. Gerrodette. 1993. The uses of statistical power in conservation biology -- the Vaquita and Northern Spotted Owl. Cons. Bio. **7**:489-500.

Trombulak, S. C., and C. A. Frissell. 2000. Review of ecological effects of roads on terrestrial and aquatic communities. Cons. Bio. **14**:18-30.

Tushingham, A. M. 1992. Observations of postglacial uplift at Churchill, Manitoba. Can. J. Earth. Sci. **29**:2418-2425.

Twenhofel, W. S. 1952. Recent Shore-line changes along the Pacific coast of Alaska. Am. Journ. Sci. **250**:523-548.

U.S. Environmental Protection Agency 2002. Guidance for developing quality systems for environmental programs. EPA QA/G-1 (EPA/240/R-02/008). United States Environmental Protection Agency, Washington, D.C.

U.S. Fish and Wildlife Service. 1994a. Endangered and threatened wildlife and plants: 90-day finding and commencement of status review for a petition to list the Alexander Archipelago wolf. Federal Register **59**:26476.

U.S. Fish and Wildlife Service. 1994b. Endangered and threatened wildlife and plants: 90-day finding for a petition to list the Queen Charlotte goshawk and request for additional information. Federal Register **59**:44124.

U.S. Fish and Wildlife Service. 1997a. Endangered and threatened wildlife and plants: 12-month finding for a petition to list the Alexander Archipelago wolf as threatened and to designate critical habitat. Federal Register **62**:46079-46710.

U.S. Fish and Wildlife Service 1997b. Petition to list the Queen Charlotte goshawk under provisions of the Endangered Species Act, 12-month finding. Memorandum to Director of Endangered Species from Regional Director. Prepared by U.S. Fish and Wildlife Service, Endangered Species, Fairbanks, Alaska.

USDA Forest Service. 1982. 36 CFR Part 219, National Forest Land and Resource Planning. Federal Register **47**:43026-43052.

USDA Forest Service 1992. Channel type user guide, Tongass National Forest, Southeast Alaska. Publication R10-TP-26. USDA Forest Service, Alaska Region, Juneau, Alaska.

USDA Forest Service 1997. Tongass National Forest land and resource management plan. USDA Forest Service, Alaska Region, Juneau, Alaska.

USDA Forest Service 1999. Sustaining the peoples' lands: recommendations for stewardship of the National Forests and Grasslands into the next century. Committee of Scientists, USDA Forest Service, Washington, D.C.

USDA Forest Service 2000. Tongass National Forest annual monitoring and evaluation report for fiscal year 1999. Publication R10-MB 414. USDA Forest Service, Alaska Region, Juneau, Alaska.

USDA Forest Service 2001a. Aquatic Ecosystem Management Handbook. USDA Forest Service Region 10, Juneau, Alaska.

USDA Forest Service 2001b. Tongass National Forest annual monitoring and evaluation report for fiscal year 2000. Publication R10-MB 431. USDA Forest Service, Alaska Region, Juneau, Alaska.

USDA Forest Service. 2002a. 36 CFR Part 219, National Forest Land and Resource Planning: Proposed Rules. Federal Register **67**:72770-72816.

USDA Forest Service 2002b. Annual report 2002: interagency regional monitoring. Publication R6-RPM-TP-02-03. USDA Forest Service, Pacific Northwest Region, Portland, Oregon.

USDA Forest Service 2002c. Tongass National Forest annual monitoring and evaluation report for fiscal year 2001. Publication R10-MB 458. USDA Forest Service, Alaska Region, Juneau, Alaska.

USDA Forest Service 2003. Tongass National Forest annual monitoring and evaluation report for fiscal year 2002. Publication R10-MB 478. USDA Forest Service, Alaska Region, Juneau, Alaska.

Vucetich, J. A., T. A. Waite, and L. Nunney. 1997. Fluctuating population size and the ratio of effective to census population size. Evolution **51**:2017-2021.

Wade, M. J. 1980. Effective population size: the effects of sex, genotype, and density on the mean variance of offspring numbers in the flour beetle, *Tribolium castaneum*. Genetical Research **36**:1-10.

Walters, C. 1997. Challenges in adaptive management of riparian and coastal ecosystems. Cons. Ecol. **1**:1. URL: http://www.consecol.org/vol1/iss2/art1.

Walters, C. J., and P. Cahoon. 1990. Large-sale management experiments and learning by doing. Ecology **71**:2060-2068.

Waples, R. S. 1991. Pacific salmon, *Oncorhynchus* spp., and the definition of "species" under the Endangered Species Act. Marine Fisheries Review **53**:11-22.

Waples, R. S. 2002. Definition and estimation of effective population size in the conservation of endangered species. Pages 147-168 in S. R. Beissinger, and D. R. McCullough, editors. Population Viability Analysis. University of Chicago Press, Chicago.

Warren, M. L., Jr., and M. G. Pardew. 1998. Road crossings as barriers to small-stream fish movement. Trans. Amer. Fish. Soc. **127**:637-644.

Waters, J. M., and G. P. Wallis. 2001. Cladogenesis and the loss of the marine life-history phase in freshwater galaxiid fishes (Osmeriformes: Galaxiidae). Evolution **55**:587-597.

Weaver, J. C. 1995. Indicator species and scale of observation. Cons. Bio. **9**:939-942.

Weir, B. S., and C. C. Cockerham. 1984. Estimating F-statistics for the analysis of population structure. Evolution **38**:1358-1370.

Wenburg, J. K., P. Bentzen, and C. J. Foote. 1998. Microsatellite analysis of genetic population structure in an endangered salmonid: the coastal cutthroat trout (*Oncorhynchus clarki clarki*). Molecular Ecology **7**:733-749.

Wenburg, J. K., J. B. Olsen, and P. Bentzen. 1996. Multiplexed systems of microsatellites for genetic analysis in coastal cutthroat trout (*Oncorhynchus clarki clarki*) and steelhead (*Oncorhynchus mykiss*). Molecular Marine Biology and Biotechnology **5**:273-283.

White, G. C., K. P. Burnham, D. L. Otis, and D. R. Anderson 1978. Users manual for program CAPTURE. Utah State Univ. Press, Logan, Utah.

Woodsmith, R. D., J. R. Noel, and M. L. Dilger. *in press*. An approach to effectiveness monitoring of floodplain channel aquatic habitat: channel condition assessment. Landscape and Urban Planning.

Woody, C. A., J. Nelson, and K. Ramstad. 2002. Clove oil as an anaesthetic for adult sockeye salmon: field trials. J. Fish Biol. **60**:340-347.

Worley, I. A., and D. Jaques. 1975. Subalpine fir (*Abies lasiocarpa*) in coastal western North America. Northwest Science **47**:265-273.

Wright, S. 1969. Evolution and the genetics of populations, volume 2: the theory of gene frequencies. University of Chicago Press, Chicago, Illinois.

Wyatt, B. 1959. Observations on the movements and reproduction of the Cascade form of cutthroat trout. Unpublished M.S. thesis, Oregon State University, Corvallis, Oregon.

Yehle, L. A. 1974. Reconnaissance engineering geology of Sitka and vicinity, Alaska, with emphasis on evaluation of earthquake and other geologic hazards. USDI - Geological Survey, Open File Report 74-53. 104 p.

Yehle, L. A. 1978. Reconnaissance engineering geology of the Petersburg Area, Alaska, with emphasis on geologic hazards. USDI - Geological Survey, Open File Report 78-675. 95 p.